Chapter **3**

DRIVERS AFFECTING BIOLOGICAL INVASIONS[1]

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THIS CHAPTER SHOULD BE CITED AS:
Hulme, P. E., Ikeda, T., Vandvik, V., Blanchard, R., Camacho-Cervantes, M., Herrera, I., Koyama, A., Morales, C. L., Munishi, L. K., Pallewatta, P. K. T. N. S., Per, E., Pergl, J., Ricciardi, A., and Xavier, R. O. (2023). Chapter 3: Drivers affecting biological invasions. 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.7430727

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DRIVERS AFFECTING BIOLOGICAL INVASIONS

EXECUTIVE SUMMARY

1 The IPBES conceptual framework, which classes drivers as either indirect or direct with respect to their impact on nature, can be adapted to address biological invasions *(well established)* {3.1.3}. The IPBES conceptual framework distinguishes between direct drivers of change in natureand indirect drivers, which are societal factors that act on biodiversity and ecosystems through influencing one or more direct drivers {3.1.3}. Biological invasions are facilitated by a broad range of direct drivers {3.3}. As invasive alien species are both intentionally and unintentionally moved by people, some indirect drivers of change in nature, such as trade or travel, can facilitate the transport and introduction of invasive alien species to new regions *(well established)* {3.2.3.1, 3.2.3.2, 3.2.3.3, 3.2.3.4}. Since invasive alien species are part of and interact with nature, changes in the biosphere can also facilitate biological invasions, for example, biodiversity loss can lead to reduced biotic resistance of ecosystems to invasive alien species, and invasive alien species can facilitate the establishment and spread of other alien species *(well established)* {3.3.5, 3.4.2}. Natural drivers, such as tsunamis or hurricanes, are known to facilitate the establishment and further spread of invasive alien species *(well established)* {3.4.1}. By incorporating aspects specific to invasive alien species within the IPBES conceptual framework, this chapter allows a comprehensive assessment of all factors influencing biological invasions **(Figure 3.3)**.

2 Indirect and direct drivers of change in nature play significant but varying roles across all stages of the invasion process *(well established)* {3.1.4, 3.2, 3.3, 3.6.2}. Indirect drivers such as sociocultural norms (particularly human values), demography (human population and migration), economic aspects (especially trade and travel), science and technology (including research) and governance (including unintended consequences of policies that inadvertently facilitate biological invasions) tend to play a stronger role in the transport and introduction stages of the invasion process *(well established)* {3.2, 3.6.2}. In contrast, the five broad classes of direct drivers examined, land- and sea-use changes (resulting from agriculture, forestry and aquaculture), direct exploitation of natural resources (mining and species harvest), pollution (eutrophication and marine plastics), climate change and invasive alien species are all more influential in the establishment and spread of invasive alien species *(established but incomplete)* {3.3, 3.6.2}.

3 The magnitude of most drivers of change in nature have increased significantly since 1950, contributing to the increase of invasive alien species globally *(well established)* {3.1.1}. Recent decades have been characterized by increases in global trade and travel, human population size and urbanization, land- and sea-use change, habitat and biodiversity loss and degradation, direct exploitation of natural resources and pollution, and global temperatures along with shifts in precipitation patterns *(well established)* {3.1.1} **(Figure 3.1)**. This sustained growth in many of the key drivers affecting the transport, introduction, establishment and spread of invasive alien species underlies recent increases in the rates of introduction, establishment and spread of invasive alien species globally *(well established)* {3.2.1, 3.6.2}.

4 International trade is the most significant driver responsible for the transport and introduction of invasive alien species across the globe *(well established)* {3.2.3.1, 3.6.2}. International trade, primarily maritime transport of commodities, has been responsible for the transport and introduction of numerous invasive alien species in both terrestrial and aquatic biomes *(well established)* {3.2.3.1}. Invasive alien species can be the commodity traded, such as ornamental plants, contaminants of commodities, such as weed seeds in grain shipments, or stowaways on shipping containers or vessels, such as biofoulants *(well established)* {3.2.3}. Historically, intentional as well as unintentional introductions through the release or escape of plants, animals and microbial organisms from agriculture, aquaculture, forestry, fisheries and non-commercial uses, have resulted in the establishment and spread of alien species in terrestrial, aquatic and marine ecosystems worldwide *(well established)* {3.3.1.1}. Biofouling and ballast water discharges have had a major influence on biological invasions in coastal marine ecosystems *(well established)* {3.2.3.1}. International trade also influences other drivers of change in nature that facilitate biological invasions, for example by promoting urbanization around major trade ports, driving land- and sea-use changes and direct exploitation of natural resources to meet international market demands, and increasing atmospheric and aquatic pollution *(well established)* {3.2.3.1, 3.2.2.3, 3.3.1, 3.3.2, 3.3.3}.

5 Land-use changes are the most significant drivers accelerating the establishment and spread of invasive alien species *(well established)* {3.3.1, 3.6.2}. Land-use changes are major drivers facilitating invasive alien species by providing opportunities for colonization, establishment and spread of alien species in both terrestrial and coastal environments worldwide *(well established)* {3.3.1}. Land-use changes related to food, fodder and biomass production facilitate the biological invasion process through the replacement of native ecosystems by monocultures of introduced crops and livestock and through intensification and changes in disturbance regimes *(well established)* {3.3.1.1, 3.3.1.2, 3.3.1.5, 3.3.1.6}. Land-use changes related to industry, infrastructure and urban development facilitate biological invasions through creation of corridors and artificial surfaces in terrestrial and coastal environments and more generally through landscape degradation *(well established)* {3.3.1.3, 3.3.1.4, 3.3.1.6}. Fragmented and degraded ecosystems are often vulnerable to colonization and spread by generalist invasive alien species *(well established)* {3.3.1.2, 3.3.1.3}.

6 **Many of the drivers known to negatively impact nature and nature's contributions to people also facilitate the introduction and spread of invasive alien species, potentially causing positive feedback loops *(established but incomplete)* {3.5}.** Increasing and expanding trade and rapid population and economic growth are global phenomena that facilitate the transport and introduction of invasive alien species worldwide, while increasing urbanization, land- and sea-use changes, pollution, ecosystem degradation and biodiversity loss are changes which again facilitate the establishment and spread of invasive alien species *(established but incomplete)* {3.2.2, 3.2.3, 3.3.1, 3.3.3, 3.4.1, 3.4.2, 3.5.3}. Such positive feedback loops between drivers remain poorly understood but are critical to understanding and addressing complex spatial patterns and temporal dynamics in biological invasions *(established but incomplete)* {3.1.5, 3.2.1, 3.2.3.1, 3.2.3.2, 3.3.4, 3.5, 3.6.1}.

7 **Historically important drivers of change in nature such as trade, land-use change and direct exploitation of natural resources remain major causes of invasive alien species introduction and spread but the role of climate change and biodiversity loss will increasingly shape future global trends in invasive alien species, potentially with a significant temporal lag *(established but incomplete)* {3.2.3, 3.3.1, 3.3.2, 3.3.4, 3.4.2}.** While some countries are moving away from intentional introductions of alien species for uses in agriculture, aquaculture, forestry, horticulture, fishing, hunting and ornamental purposes, other countries do not effectively regulate and manage the use of invasive alien species for these purposes, resulting in sustained or increased rates of introduction and spread in affected regions *(established but incomplete)* {3.2.5, 3.2.3.2, 3.3.1.1}. The increasing role of climate change and biodiversity loss in facilitating the establishment and spread of invasive alien species is indicative that past patterns of biological invasions may not be a good guide to future patterns *(well established)* {3.3.4, 3.4.2}. Furthermore, there will be a vast legacy of future invasions (invasion debt) caused by significant time lags in the response of invasive alien species to drivers of change in nature, and the ongoing intensification of many drivers are responsible for increases in this legacy *(established but incomplete)* {3.1.1, 3.1.5}.

8 **Despite major inequalities in wealth worldwide, economic growth facilitates biological invasions in both developed and developing countries *(established but incomplete)* {3.2.3}.** Countries with high levels of consumption tend to expedite the introduction and establishment of alien species, and the cumulative build-up of assets, which support greater consumption, may lead to more immediate increases in numbers of alien species *(established but incomplete)* {3.2.3.6}. Poverty and marginalization created by economic inequality within and among countries may indirectly drive the introduction, establishment and spread of invasive alien species *(well established)* {3.2.3.6}. For those countries with a lower level of wealth, trends suggest that as economies grow and larger asset bases are built, so the risk of invasive alien species introductions might increase *(established but incomplete)* {3.2.3.6}. Risks may also be exacerbated where the route to economic growth and poverty reduction encourages the development of economic sectors based around invasive alien species *(established but incomplete)* {3.2.3.6}. This appears to be a major issue for Indigenous Peoples and local communities who in some cases may have few options but to use invasive alien species for food, fibre and also medicines *(established but incomplete)* {3.2.3.6}.

9 **Many Indigenous Peoples and local communities have a good and holistic understanding of the drivers facilitating invasive alien species on their lands *(well established)* {3.2, 3.3, 3.5} (Box 3.6, Box 3.15).** Indigenous Peoples and local communities point to how policies, governance and institutions aimed at improving livelihoods and the environment may inadvertently cause the introduction of invasive alien species *(established but incomplete)* {3.2.5, 3.2.3.6, 3.3.1.13} **(Box 3.6, Box 3.15)**. For example, they report that promotion of alien species for food, fibre, income generation, or medicinal purposes may act as a driver facilitating biological invasions *(well established)*, and such invasions can be especially facilitated in situations where native biodiversity, including species they traditionally depended on for these benefits, have declined *(established but incomplete)* {3.2.3.6, 3.2.5}. In some cases, Indigenous Peoples and local communities observe that urban areas or anthropogenic corridors act as sources of further spread of invasive species into their lands *(established but incomplete)* {3.2.2, 3.3.1.7}, and they also recognize land-abandonment, sometimes coupled with natural drivers or climate extremes, as responsible for the spread of alien species *(established but incomplete)*

{3.3.1.5.1}. Indigenous Peoples and local communities are well aware that drivers interact in complex ways to drive biological invasions *(well established)* {3.5}. Indigenous Peoples and local communities also identify challenges of land tenure and access rights as significant factors limiting the extent to which they can address invasive alien species on their lands *(established but incomplete)* {3.2.5}. Overall, Indigenous Peoples and local communities broadly align in understanding of the relative importance of drivers and trends in invasive alien species with reports from the scientific literature *(established but incomplete)* **(Box 3.15)**.

10 **Few drivers act in isolation, and interactive effects appear to be crucially important, but few studies have examined the interactive effects of several co-occurring drivers in facilitating invasive alien species *(established but incomplete)* {3.1.5, 3.5, 3.6.1, 3.6.3}.** There are potentially many multiplicative interactions among drivers that are likely to lead to unprecedented invasion scenarios *(established but incomplete)* {3.1.6, 3.5, 3.6.3}. Yet fewer than 5 per cent of studies examining drivers of biological invasions addressed more than one driver *(well established)* {3.1.6, 3.6.1}. Stakeholders, including decision makers, are currently inadequately prepared to address and react to unexpected consequences arising from additive or multiplicative effects of several drivers on the transport, introduction, establishment and spread of invasive alien species *(established but incomplete)* {3.5, 3.6.3}.

11 **Knowledge is biased towards only a subset of drivers, and less is understood regarding how indirect drivers of change in nature influence biological invasions compared to direct drivers *(well established)* {3.6.1}.** While this chapter summarizes the available evidence of the role of each direct and indirect driver on biological invasions, the underlying knowledge base is biased *(well established)* {3.6.1}. Most of the recent research addressing the role of drivers in facilitating biological invasions has focused on a subset of drivers, especially economic drivers such as trade and transport, climate change and land-use change *(well established)* {3.6.1}. The importance of sociocultural values and unintended consequences of governance, policy and insitutions in shaping biological invasion remains understudied *(well established)* {3.6.1, 3.6.3}.

12 **Biases in the availability of data on how drivers of change in nature influence biological invasions highlight that causal factors are most poorly understood for regions potentially most exposed to increasing risks from invasive alien species *(well established)* {3.6.1}.** This chapter examines a variety of sources, including Indigenous and local knowledge, and explicitly includes evidence of biological invasions across multiple geographic regions, taxonomic groups and biomes {3.1.2, 3.6.1}. Nevertheless, the evidence base for how drivers influence biological invasions is largely drawn from developed countries, particularly in Europe, North America and Oceania, terrestrial temperate ecosystems and plants, and there is a lack of information for polar regions and developing countries, especially sub-Saharan Africa, tropical Asia and South America, marine systems and other taxonomic groups *(well established)* {3.6.1, 3.6.3}.

3.1 INTRODUCTION

The concept of direct and indirect drivers of change in nature has been a cornerstone in all the assessments led by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) to date (Díaz *et al.*, 2015; IPBES, 2016a, 2018f, 2018e, 2018c, 2018d, 2019; Nelson *et al.*, 2006), and the intention in this chapter is not to repeat past material pertaining to the status and trends in the drivers, but to synthesize information on the role of drivers of change in nature in affecting the biological invasion process. Chapter 3 therefore focuses on identifying how different drivers of change in nature affect the transport, introduction and establishment of invasive alien species (**Glossary**; **Box 3.1**). Chapter 3 builds on the status and trends of alien species, and the subset of these termed invasive alien species, documented in **Chapter 2**, with a more in-depth focus on establishing the drivers behind these patterns. The information provided in Chapter 3 contributes to the understanding of the underlying causes of the increase in invasive alien species globally (**Chapter 2**), the impacts of invasive alien species on nature, nature's contributions to people and good quality of life (**Glossary**; **Chapter 4**) and underpins management actions (**Glossary**; **Chapter 5**) and policy options for the prevention and control of invasive alien species and their impacts (**Glossary**; **Chapter 6**).

3.1.1 Setting the scene: increasing global trends in drivers of change in nature

The size and environmental footprint of the world's human population has grown dramatically over the past two centuries, with rates of change accelerating over the past few decades (Steffen *et al.*, 2015). This "great acceleration" (Steffen *et al.*, 2015) can be discerned across a majority of direct and indirect drivers of change in nature, which are of relevance to the increasing trends in the number and abundance of invasive alien species globally (**Chapter 2**). The number of people in the world has grown from 3.7 billion in 1970 to an estimated 7.7 billion in 2019 **(Figure 3.1)**, and while population growth is slowing, a global population of 10 billion may be reached by 2050 (UNEP, 2019; United Nations *et al.*, 2019). An increasing proportion of the global population is living in urban

Box 3 1 **Rationale of the chapter.**

Chapter 3 provides an analysis and synthesis of how direct and indirect anthropogenic drivers of change in nature, along with natural drivers and biodiversity loss itself, are responsible for the transport, introduction, establishment and spread of invasive alien species. The chapter first outlines the conceptual and analytical framework and approaches, then synthesizes the evidence for the role each driver plays across the biological invasion process (**Glossary**), before synthesizing the knowledge and identifying data gaps. Invasive alien species are one of five major classes of direct drivers of change in nature identified by the Global Assessment of Biodiversity and Ecosystem Services (IPBES, 2019), and are the theme of this assessment. Unlike other drivers, invasive alien species are both a direct driver of change in nature and they are integral parts of nature. As a consequence, invasive alien species can be directly affected by drivers that are classified as indirect drivers of change in nature, and invasive alien species along with biodiversity loss can facilitate invasion by other alien species.

Guiding questions:

- What are the main direct and indirect drivers responsible for the introduction, spread, abundance and dynamics of invasive alien species for each invasion stage and taxon?
- How rapidly are potential drivers changing compared to the last 30 years and which drivers are changing most rapidly?

Keywords:

Indirect drivers of change in nature, direct drivers of change in nature, invasive alien species, demographic drivers, economic drivers, science and technological drivers, policies, governance and institutions as drivers, land- and sea-use change, natural resource extraction, pollution, climate change, natural drivers, biodiversity loss, ecosystem resilience, interacting drivers, Indigenous Peoples and local communities.

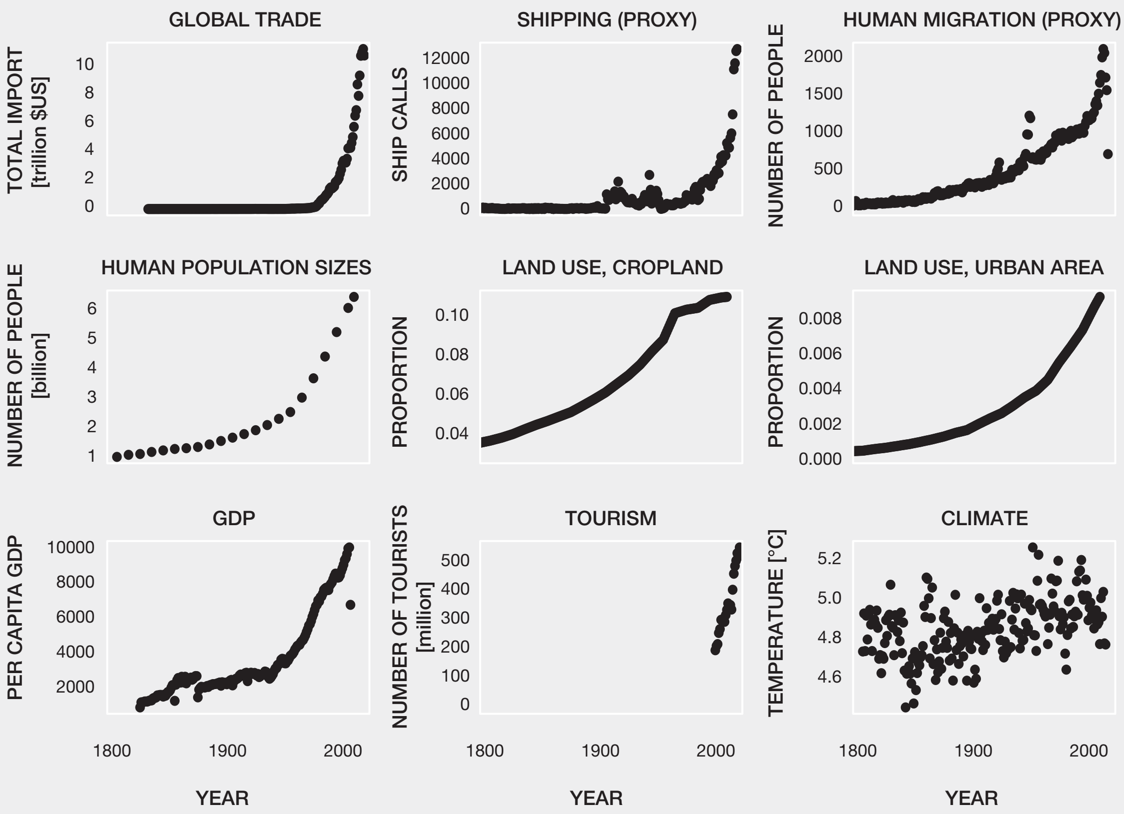


Figure 3 1 **Trends in a selection of drivers and correlates of biological invasions.**

Panels show temporal trends for some of the main drivers and correlates of biological invasions averaged globally. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7615582 areas – the total area of urban settlements has grown by approximately 2.5 times since 1970, accounting for 7.6 per cent of the global land area and housing 3.5 billion people in 2015 (Shukla *et al.*, 2019; UNEP, 2019). Human migration and travel are also increasing **(Figure 3.1)**. Meanwhile, the global economy has grown nearly fivefold over the last 50 years **(Figure 3.1)**, a growth that is projected to continue. This economic growth has been fuelled by an increase in global primary energy production of more than 270 per cent over the same period, of which fossil fuels still contribute more than 80 per cent (IEA, 2020). Consumption has tripled and global trade grown nearly tenfold in the last 50 years **(Figure 3.1)**, with shifting patterns of consumption and production across regions, and increases in transport of goods and people (**Figure 3.1**; IPBES, 2019).

These global population and economic drivers are having dramatic impacts on our lands and seas (IPBES, 2022c). Close to 75 per cent of ice-free land areas and 60 per cent of the oceans are significantly impacted by people, and agricultural crop production has increased by about 300 per cent since 1970, with crops now occupying half of the habitable land on Earth (IPBES, 2019). Of the more than 50,000 wild species harvested for use as food, energy, medicine, materials, income generation, or other uses globally, only 34 per cent are used sustainably (IPBES, 2022c). Water extraction, predominantly for irrigation of agricultural crops, grew by nearly 65 per cent from 1970 to 2010, and over the same period mining of metal ores increased by three and a half times and mining for sand, gravel and clay increased by nearly five times (IRP, 2019). Approximately 60 billion tonnes of renewable and non-renewable resources are now extracted globally every year, having nearly doubled since 1980 (IPBES, 2019). Up to 400 million tonnes of heavy metals, solvents, toxic sludge and other industrial wastes are dumped annually into the

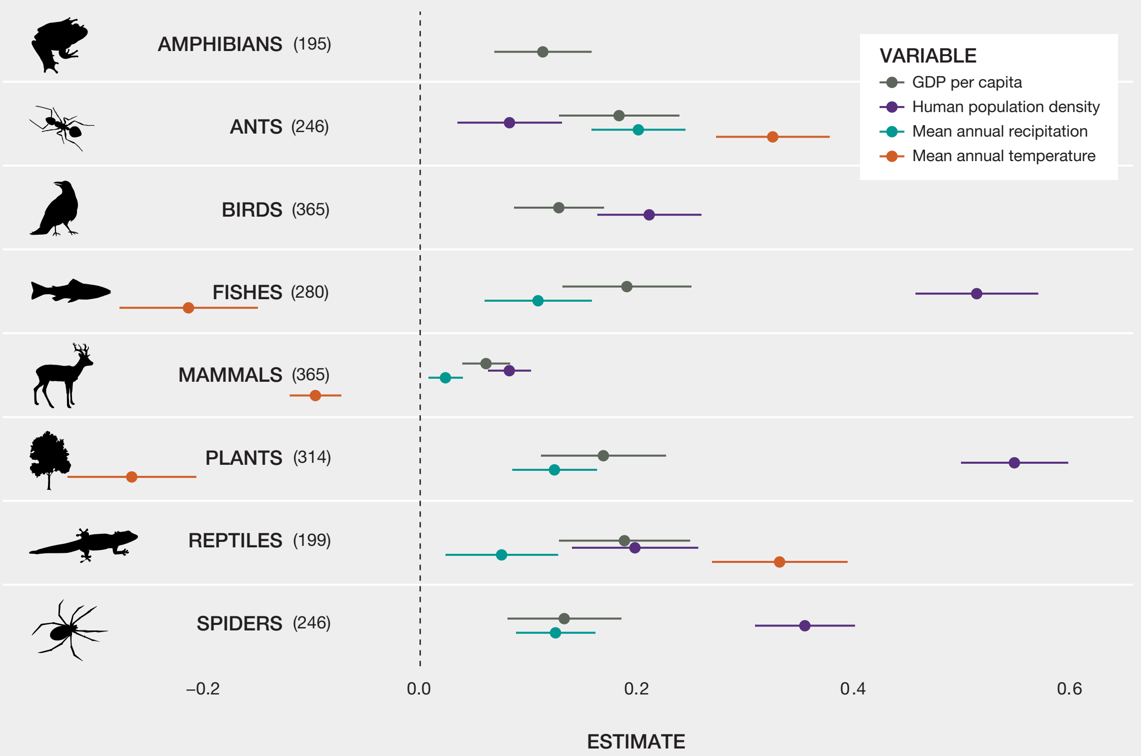


Figure 3 2 **Estimated effects of different factors on established alien species richness across eight taxonomic groups: amphibians, ants, birds, freshwater fishes, mammals, vascular plants, reptiles and spiders (from top to bottom).**

The results of linear mixed models indicate the effects of different factors (GDP per capita; human population density; mean annual precipitation; and mean annual temperature) on alien species (**Glossary**) richness within eight taxonomic groups across 423 mainland regions. Number in parentheses are numbers of regions included per taxonomic group. Overall, taxonomic groups respond differently to the effects of climate and gross domestic product (GDP) per capita, but human population density is consistently among the best predictors with especially high effects for fish, plants and spiders. Estimates (±1 standard error) – represented by dots and lines – of effects were obtained from linear mixed-effects models of ln (species richness + 1), with subcontinental regions nested within continents as random effects. Adapted from Dawson *et al.* (2017) https://doi.org/10.1038/s41559-017-0186, under license CC BY 4.0.

world's waters (UNEP, 2019; IPBES 2019). Nitrogen fluxes to aquatic ecosystems (**Glossary**) have increased up to 20-fold in the last decade (IPBES, 2019). Marine plastic pollution has increased tenfold since 1980, and is found in all oceans at all depths, concentrating in ocean currents (UNEP, 2019).

Accelerating human impacts are changing the Earth's ecosystems and climate at unprecedented rates, to the extent that they are now dominating Earth system processes (IPBES, 2019). Climate has warmed by 1.1°C on average, and is projected to reach at least 1.5°C within the next three decades, and climate change is contributing to changed precipitation patterns, sea level rise, increasing fire risk (**Glossary**) and a higher frequency of extreme events in many regions (IPCC, 2021, 2022). Ecosystems are degrading at unprecedented rates, with climate change exacerbating other threats (Pörtner *et al.*, 2021; **Chapter 4**, **Box 4.5**). This degradation of biodiversity and ecosystems is impacting ecosystem functioning and harming nature's ability to support human well-being (IPBES, 2019, 2022c; IPCC, 2022). A majority of these direct and indirect drivers of change in nature are affecting, and often facilitating, invasive alien species, which are increasing at accelerating rates globally (**Chapter 2**, **Figure 2.2**). The aim of Chapter 3 is to address how these drivers affect the transport, introduction, establishment and spread of invasive alien species.

Drivers do not act in isolation; status and trends in nature are the outcome of the often multiplicative effects of many co-occurring drivers (IPBES, 2019; **Chapter 4**, **Box 4.5**). A recent study systematically and quantitatively ranked direct drivers of change in nature (**section 3.1.2**) in terms of impacts on biodiversity and found that land-use change was generally the most important, but that relative importance of drivers varied across realms, IPBES regions and with the biodiversity components considered (Jaureguiberry *et al.*, 2022) and with scales (Bonebrake *et al.*, 2019). Invasive alien species are recognized as being a driver of change in nature and at the same time a component of biodiversity. A global meta-analysis focussing explicitly on identifying extrinsic factors related to invasive alien species richness found that that human population density of an area, which can be a proxy for multiple and often co-occurring drivers such as trade, travel and land-use, was highly correlated to the number of introduced alien amphibians, fish, plants and spiders within that area (**section 3.1.2** and **Figure 3.2**).

3.1.2 Scope and organization of the chapter with reference to the IPBES conceptual framework

The IPBES conceptual framework and Global Assessment recognize invasive alien species as one of five anthropogenic "direct drivers" of change in nature along with climate change, land- and sea-use change, pollution and direct exploitation of natural resources (Díaz *et al.*, 2015; IPBES, 2019). According to this framework, direct drivers have direct physical (mechanical, chemical, etc.) and biological (physiological, ecological, behavioural) effects on nature (biodiversity and ecosystems) which again impact nature's contributions to people (including ecosystem goods and services) and more generally good quality of life (**Chapter 1**, **Figure 1.11**; Díaz *et al.*, 2018). The IPBES invasive alien species assessment refers to these drivers as "direct drivers of change in nature". The magnitude of the impact of these direct drivers of change on nature, and in some cases on nature's contributions to people and good quality of life, is also shaped by five "indirect drivers" of change: human demography, economic development, technological change, the strength of national and international governance (**Glossary**) as well as sociocultural factors **(Figure 3.3)**. These drivers are described as indirect because they do not directly impact nature (i.e., biodiversity and ecosystems), but act through one or more direct drivers of change in nature (Nelson *et al.*, 2006). Indirect drivers impact nature by affecting the level (e.g., magnitude), direction (e.g., increase or decrease) or rate (e.g., change over time) of the direct drivers. For example, the impacts of economic growth (an indirect driver of change in nature) affects biodiversity or ecosystems through the effects of one or more direct drivers, such as land-use change or pollution.

The classification of drivers outlined through the IPBES conceptual framework has proven useful for synthesis and cross-assessment referencing (e.g., IPBES, 2019; Pörtner *et al.*, 2021) but requires specific consideration for this assessment because invasive alien species are simultaneously the focus of the IPBES invasive alien species assessment and one of the five anthropogenic direct drivers of change in nature (**Figure 3.3**; **Chapter 1**, **section 1.6.1**). This implies that indirect drivers of change in nature may directly affect invasive alien species. For example, international trade is classified as an indirect driver of change in nature, yet an important consequence of trade is that it increases the number of invasive alien species introductions worldwide (Hulme, 2021b), and it does so by directly facilitating the transport and introduction of invasive alien species **(Figure 3.3)**. The process of biological invasions (including all stages: transport, introduction, establishment and spread of invasive alien species; **Glossary**) is also influenced by the five anthropogenic direct drivers of change in nature, including interactions amongst invasive alien species (e.g., by causing "invasional meltdown", **Glossary**; **section 3.3.5.1**; **Chapter 1**, **section 1.3.4**). All five primary direct anthropogenic drivers are therefore also considered in this assessment.

In addition to the main anthropogenic direct and indirect drivers recognized by the IPBES framework, biological invasions can be further facilitated by natural drivers and in particular natural hazards such as tsunamis, floods, fire and hurricanes. While the involvement of human activities within the biological invasion process is inherent to the definition of alien species (**Chapter 1**, **Figure 1.1**), these natural drivers can play a major role in both the introduction of alien species from one region where they are alien to new regions, and also aid their establishment and further spread within regions where they are already present as alien species. A further driver not directly addressed in previous IPBES assessments is biodiversity loss, but in the case of invasive alien species it can be seen as a driver that facilitates their establishment and spread, as a result of reduced resistance of altered natural ecosystems to invasive alien species (**Chapter 1**, **section 1.4.3**). Thus, the transport, introduction, establishment and spread of invasive alien species can be facilitated by both direct and indirect anthropogenic drivers of change in nature, as well as by natural drivers and by biodiversity loss. These drivers do not act in isolation but may interact with each other in different and complex ways (**section 3.1.5**). In part as a result of these complexities, the knowledge base is both limited and fragmented, and attribution of cause-effect relationships can be challenging (**sections 3.1.5**, **3.6.1**). To acknowledge and cover these complexities and limitations, the assessment is organized as follows:

Section 3.2 assesses the role that five indirect drivers of change in nature play in the different stages (transport, introduction, establishment and spread) of the biological invasion process **(Table 3.1)**. The indirect drivers examined are:

- sociocultural drivers and social values (including norms, traditions, cultural beliefs, desires, perceptions);
- demographic (including human population density, migration, international crises and urbanization);
- economic (such as international trade and travel, externalities and wealth, inequality and poverty);
- science and technology (including research and communication and breeding/genomic technology);
- policies, governance and institutions (note that Chapter 3 focuses on the unintended facilitation of biological invasions by policies, governance and institutions targeting other societal objectives (i.e., "perverse incentives", *sensu* IPBES, 2019). Policies, governance and institutions explicitly dealing with biological invasions are dealt with in **Chapter 6**).

Section 3.3 examines the role of the five direct drivers of change in nature in influencing the distribution and abundance of invasive alien species **(Table 3.1)**:

- land- and sea-use changes (including introductions from the direct use of alien species in terrestrial, aquatic and marine bioproduction systems as well as landscape and seascape fragmentation, disturbance and deterioration);
- direct exploitation of natural resources (such as species harvesting, hydrological resource harvesting and mining);
- pollution (including eutrophication and nutrients, other contaminants, marine debris and solid waste);
- climate change (including changes in temperature and precipitation regimes and extremes, carbon dioxide (CO_2) enrichments in air and water, fire regimes, sea level rise and assisted colonization);
- invasive alien species (through biotic facilitation and biological control; **Glossary**).

As explained above, two additional drivers are also considered in section 3.4:

- natural hazards (such as hurricanes, earthquakes, tsunamis).
- biodiversity loss and ecosystem resilience (notably reduced biotic resistance to invasion; Glossary).

Section 3.5 then examines multiple, additive or interacting effects among drivers, especially among anthropogenic direct drivers. Due to knowledge gaps (**section 3.6.1**) this section does not provide an exhaustive assessment but focuses on four illustrative examples of two- or three-way multi-driver impacts and their consequences for biological invasions.

Each subsection within sections 3.2 to 3.5 first briefly describes the trends (**Glossary**) and status of the driver(s) considered, then assesses the overall effects of this driver on the transport, introduction, establishment and spread of invasive alien species and, where there is information, notes specific effects on particular biomes, taxa and units of analysis. Due to the complexities of relationships among drivers and biological invasions coupled with the limited knowledge available (**sections 3.1.3** to **3.1.5**, **Figure 3.3**), a systematic literature search across all topics relevant to the chapter was not feasible, and targeted but coordinated literature searches were conducted instead (**section 3.6.2** for details).[2] In these searches, knowledge was extracted from a broad range of sources, including published scientific literature and reports, and the searches were augmented with literature from the cross-chapter literature review[3] on Indigenous Peoples and local communities and invasive

2. Data management report available at: https://doi.org/10.5281/zenodo.5529309
3. Data management report available at: https://doi.org/10.5281/zenodo.5760266

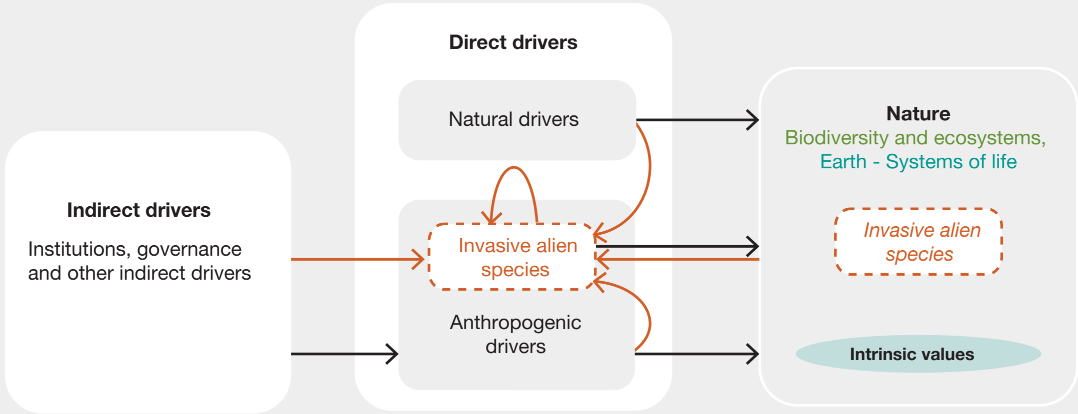


Figure 3 3 **Schematic illustration of how invasive alien species can be influenced by indirect drivers of change in nature, anthropogenic and natural direct drivers of change in nature and by changes to nature (i.e., loss of biodiversity or ecological resilience).**

The assessment builds on the IPBES conceptual framework (Díaz *et al.*, 2015) under license CC BY-NC-SA 3.0, adding focus and detail around how changes to drivers and to nature may influence invasive alien species (lighter arrows). Invasive alien species are classified as one of five direct anthropogenic drivers of change in nature; therefore, they can be influenced both directly and indirectly (*via* other direct drivers) by indirect drivers of change in nature. Biological invasions may also be influenced by all direct drivers of change in nature, including invasive alien species, and by natural drivers (especially natural hazards). Finally, there can also be feedbacks from nature (biodiversity and ecosystems) to invasive alien species, for example, biodiversity loss or invasive alien species can make ecosystems less resistant to further invasive alien species. Invasive alien species are therefore both a driver of change in nature and part of nature (dotted lines). Lighter arrows indicate the focal causal relationships of this chapter, within the context of the IPBES conceptual framework, darker arrows denote additional causal links among drivers and between drivers and nature covered in the IPBES Global Assessment (IPBES, 2019).

alien species. Finally, the authors identify knowledge gaps (**section 3.6.1**) before drawing conclusions and integrating the chapter's findings on the role of drivers of change in nature in facilitating invasive alien species across biomes and realms and across the biological invasion process (**sections 3.6.2**, **3.6.3**).

3.1.3 Identifying drivers of change in nature of relevance for invasive alien species

Chapter 3 adapts the IPBES conceptual framework, recognizing that invasive alien species are, simultaneously, one of the five main direct drivers identified by IPBES (Díaz *et al.*, 2015, 2018; IPBES, 2019), and at the same time the focus of this assessment **(Figure 3.3; Table 3.1)**. Specifically, this chapter acknowledges that some indirect drivers of change in nature, and notably those related to trade, transport and travel, may in fact be directly facilitating the transport, introduction, establishment and spread of invasive alien species. Further, natural drivers, while included in the IPBES conceptual framework as a direct driver, are generally not considered in IPBES assessments (Pereira *et al.*, 2010; Díaz *et al.*, 2015, 2018; IPBES, 2019) but are known to be important factors facilitating biological invasions and are, therefore, included in this chapter (**Figure 3.3**, **section 3.4.1**). Similarly, biodiversity loss can reduce the resilience of ecosystems to invasive alien species and while not considered in the IPBES conceptual framework as a driver, the role of biodiversity loss and changes to ecosystem resilience in facilitating biological invasions is included in Chapter 3 (**section 3.4.2**). Interactions between indirect and direct drivers of change in nature, along with natural drivers and biodiversity loss, create different chains of relationships, attribution, and influences on the biological invasion process. These relationships may vary according to type, intensity, duration and distance. These relationships are captured by cross-referencing between subsections throughout the assessment, and by explicitly considering selected interactive effects (**section 3.5**).

3.1.3.1 Indirect drivers of change in nature affecting invasive alien species

Following previous IPBES assessments (IPBES, 2016a, 2018f, 2018e, 2018c, 2018d, 2019, 2022a), Chapter 3 considers a number of drivers under all five classes of indirect drivers of change in nature: sociocultural, demographic, economic, science and technological and institutional **(Table 3.1)**. It is important to note that indirect drivers of change in nature may both directly and indirectly influence the biological invasion process and the introduction, establishment and spread of invasive alien species **(Box 3.1)**. Sociocultural context, particularly values, beliefs and social norms, can exert significant pressure on decision-making regarding biological invasions (Shackleton *et al.*, 2019; **Chapter 1**, **section 1.5.2**) and is materially manifested in lifestyles and consumption patterns that can act directly in facilitating the introduction and spread of invasive alien species. Demographic drivers, including human population growth and migration, underpin all anthropogenic direct drivers of change in nature that also facilitate biological invasions through increasing urbanization. A significant economic driver that often correlates strongly with the number of alien species found in a country is economic

Table 3 1 **The indirect and direct anthropogenic drivers of change in nature and other factors affecting invasive alien species, as assessed in Chapter 3.**

The IPBES conceptual framework considers indirect and direct drivers of change in nature (Díaz *et al.*, 2015; Nelson *et al.*, 2006). Following the IPBES Global Assessment, this assessment considers five classes of indirect and five classes of direct anthropogenic drivers. In addition, the assessment considers two other classes of drivers: natural drivers and biodiversity loss. For each of these classes of drivers, the assessment considers the influence of a number of specific drivers on the transport, introduction, establishment and spread of invasive alien species. This table shows all the drivers considered in this chapter, with classes of drivers in bold, and drivers under each class in normal font (see **section 3.1.2** for more details).

INDIRECT DRIVERS Anthropogenic factors that affect nature indirectly by altering one or more direct drivers, but which may act both indirectly and directly on invasive alien species.	**ANTHROPOGENIC DIRECT DRIVERS** Factors that describe direct human influence on nature. These may affect invasive alien species directly, or *via* interactions and feedbacks involving other drivers.	**NATURAL DRIVERS AND BIODIVERSITY LOSS** Factors that describe natural drivers and aspects of biodiversity loss which may directly and in interaction with other drivers facilitate invasive alien species.
Sociocultural drivers and social values (3.2.1) **Demographic drivers (3.2.2)** • Regional and national changes in human population density • Human migration • International crises: armed conflict and emergency aid • Urbanization **Economic drivers (3.2.3)** • International trade and global commerce • Human international travel for commerce and tourism • Externalities of negative impacts and cost • Wealth, inequality and poverty **Science and Technology (3.2.4)** • Research • Development of communication technology • Breeding and genomic technologies **Policies, governance and institutions (3.2.5)**	**Land- and sea-use change (3.3.1)** • Introductions from the use of alien species in terrestrial, aquatic and marine bioproduction • Fragmentation of ecosystems • Creation of anthropogenic corridors • Deployment of marine infrastructure • Changes in landscape – seascape disturbance regimes • Landscape – seascape degradation **Direct exploitation of natural resources (3.3.2)** • Species harvesting • Hydrological resources • Fossil fuels and mining **Pollution (3.3.3)** • Eutrophication and nutrient deposition • Other contaminants in water and soil • Marine debris • Dispersal of solid waste **Climate Change (3.3.4)** • Temperature change • Precipitation change • Climate extremes • CO_2 enrichment in air, water • Fire regime changes • Sea level rise • Assisted colonization **Invasive alien species (3.3.5)** • Biotic facilitation • Biological control	**Natural drivers (3.4.1)** Natural hazards such as tsunamis, hurricanes, earthquakes, wildfire, floods and volcanic activity **Biodiversity loss and ecosystem resilience (3.4.2)**

growth, often expressed as per capita gross domestic product (GDP; Dawson *et al.*, 2017; Essl *et al.*, 2011, 2015; Hulme, 2011b), reflecting the intensity of international trade which is a major conduit for the introduction of alien species (Hulme, 2009, 2021b; Seebens *et al.*, 2015; Westphal *et al.*, 2008). While technology is a major factor in economic growth, its effect on biological invasions depends on how it is used. The use of new technologies to limit the transport, introduction, establishment and spread of invasive alien species, along with technological approaches to aid eradication and containment (**Glossary**) of invasive alien species are discussed in **Chapters 5** (**sections 5.5.3**, **5.5.4**) and **6** (**sections 6.3.3.4**, **6.7.2**). **Chapter 3** focuses on the role of technology as a driver, for example, how internet commerce (Walters *et al.*, 2006) is facilitating the introduction and spread of invasive alien species, and on how new technologies such as gene editing can potentially be used to breed species with traits that might make them more likely to be invasive (e.g., cold tolerance, pest resistance). Economic drivers are strongly linked to institutional drivers, which govern production through regulations, taxes and subsidies. The role of policies and institutions in managing biological invasions is addressed in **Chapter 6** whereas the synthesis in **Chapter 3** is restricted to how regulations, taxes and subsidies result in unintended consequences that facilitate the transport, introduction, establishment and spread of invasive alien species (**section 3.2.5**).

3.1.3.2 Anthropogenic direct drivers of change in nature affecting invasive alien species

In line with previous IPBES assessments (IPBES, 2016a, 2018f, 2018e, 2018c, 2018d, 2019, 2022a), this assessment considers the five main anthropogenic direct drivers of change in nature: land-use (including sea-use) change, direct exploitation of natural resources, pollution, invasive alien species and climate change. Land- or sea-use changes can lead to the increased introduction of alien species, either intentionally through the specific use of alien crops and livestock or unintentionally as contaminants of agricultural or aquacultural commodities. Land-use change that leads to habitat (**Glossary**) fragmentation, establishes infrastructure corridors (e.g., roads, canals) through which alien species can spread, alters the baseline rates of disturbance, or more generally degraded habitats can increase the vulnerability of native ecosystems to invasive alien species (Vilà & Ibáñez, 2011). Direct exploitation of natural resources includes both the direct exploitation of biotic resources through species harvesting as well as of abiotic resources such as water and minerals. Harvesting of top predators can lead to trophic cascades that facilitate the establishment of alien species, such as the case of overfishing in the Black Sea resulting in an outbreak of *Mnemiopsis leidyi* (sea walnut; Daskalov *et al.*, 2007). Exploitation of abiotic (e.g., mining) and biotic (e.g., deforestation) resources can drive biological invasions by altering the baseline disturbance regime, which can facilitate the invasion of alien species that are better adapted to the altered conditions (Catford *et al.*, 2012). Pollution, particularly eutrophication, can favour alien species in both aquatic (Vermonden *et al.*, 2010) and terrestrial ecosystems (Brooks, 2003). Climate change, particularly through the effects of higher temperatures and frequency of extreme events, has long been widely expected to increase the rate at which alien species are introduced, establish and spread (Walther *et al.*, 2009). Less well understood is the risk that deliberate translocation of species by humans from one region to another in order to ensure survival in the face of climate change might result in the introduction of invasive alien species (Ricciardi & Simberloff, 2009). Although including invasive alien species as a direct driver affecting biological invasions might sound like circular reasoning, there is increasing evidence of the role that invasive alien species play in facilitating other alien species at different stages of the biological invasion process, aiding dispersal and transportation or as mutualists (e.g., alien mycorrhiza, pollinators and seed dispersers), allowing their reproduction and spread. This process, by which a group of alien species facilitate one another, increasing the likelihood of survival and/or of ecological impact (Braga, Gómez Aparicio, *et al.*, 2018) and potentially causing "an accelerating accumulation of introduced species", has garnered its own term "invasional meltdown" (Simberloff, 2006, **Chapter 1**, **section 1.3.4**; **Chapter 4**, **section 4.7.2**).

3.1.3.3 Natural drivers and biodiversity loss as direct drivers affecting biological invasions

Changes in biodiversity and ecosystems due to natural drivers (including natural hazards) are viewed as innate and integral processes and components of nature itself, and have thus not been extensively considered in prior IPBES assessments (e.g., IPBES, 2019). However, natural drivers can play a significant direct role in the transport, introduction, establishment and spread of invasive alien species both within and beyond their prior invaded range (**Glossary**). Natural large-scale disturbances, such as hurricanes, earthquakes and tsunamis can facilitate the further introduction of alien species from an existing invaded range to new regions, consequently expanding the invaded range (Carlton *et al.*, 2017) as well as facilitating their wider spread in regions where they are already present as alien species (Bellingham *et al.*, 2005). For example, hurricanes appear responsible for the spread of *Cactoblastis cactorum* (cactus moth) between Caribbean islands (Andraca-Gómez *et al.*, 2015), the expansion of *Phragmites australis* (common reed) in the Gulf of Mexico (Bhattarai & Cronin, 2014), and increased rates of recruitment and persistence of invasive alien trees in the subtropical forests of Puerto Rico (Thompson *et al.*, 2007). While native biodiversity is a major component of nature and nature's contributions to people, and thus has been considered as a key response variable in previous IPBES assessments (IPBES, 2019), for invasive alien species biodiversity loss can also be seen as a driver that facilitates biological invasions since loss of biodiversity, and especially reduced functional complexity and/or integrity of ecosystems, can reduce biotic resistance to invasive alien species (Levine *et al.*, 2004). Chapter 3 thus considers the consequences of native biodiversity loss and changes to ecosystem resilience for biological invasions, since this is known as an important feedback mechanism directly influencing the introduction, spread and establishment of invasive alien species (**Figure 3.3**; **Table 3.1**; **section 3.4.2**). This additional complexity is explicitly captured by assessing focal relationships (lighter arrows) from natural drivers and from nature to invasive alien species, in the context of the IPBES conceptual framework **(Figure 3.3)**.

3.1.4 Differential role of drivers along the stages of the biological invasion process

Biological invasions are widely viewed as processes comprising a series of sequential stages (Blackburn *et al.*, 2011; Colautti & MacIsaac, 2004; Theoharides & Dukes, 2007; **Chapter 1**, **section 1.4**). These stages capture the transport of a species to a region beyond its native range, the introduction of the species (intentionally or/ and unintentionally) into habitats in that region, and its subsequent establishment as a self-sustaining population, followed by its wider geographic spread in the invaded range (**Figure 3.4**; **Chapter 1**, **section 1.4**). Pathways of introduction are referred to by the Convention on Biological Diversity as the means by which species are moved to new regions beyond their native range (CBD, 2014; Hulme *et al.*, 2008). Pathway assessment usually focuses on movements until a species reaches the border of an administrative unit, such as a country, although is not restricted to this definition. Pathways are categorized into six major classes (release, escape, contaminant, stowaway, corridor, and unaided) with several sub-classes (CBD, 2014; **Chapter 2, Table 2.1**; **Chapter 1**, **Box 1.6**). In the transport stage, drivers can act by facilitating pathways, such as when economic growth increases trade and transport volumes, thereby facilitating transport of alien species as stowaways (**section 3.2.3**). In later stages of the biological invasion process, drivers can act both intentionally and unintentionally to facilitate the establishment and spread of invasive alien species, such as when alien species are used for or spread as pests or contaminants of goods used for bioeconomic purposes (agriculture, aquaculture, forestry, or as pets or ornamentals)

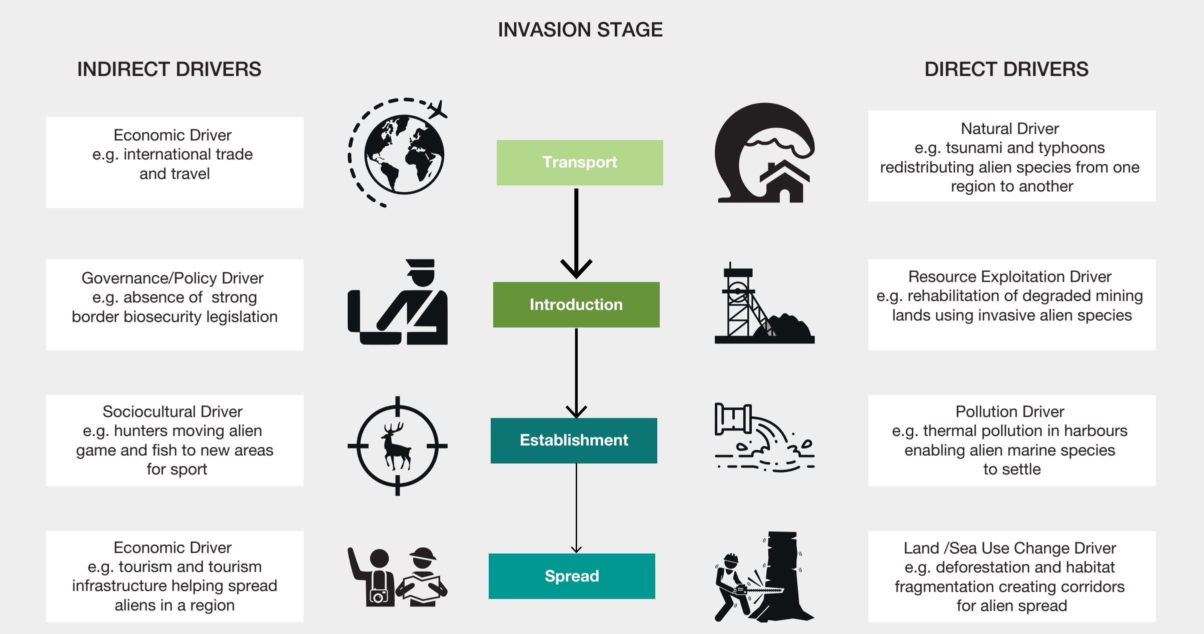


Figure 3 4 **Schematic using selected examples of how both indirect and direct drivers of change in nature may facilitate invasive alien species along four stages in the biological invasion process: transport, introduction, establishment and spread.**

The examples are meant to be illustrative and not an exhaustive set of scenarios with several drivers mentioned also influencing other stages. See **section 3.6.2** for a synthesis of the influence of different drivers on invasive alien species across stages of the biological invasion process, biomes and realms.

or when land-use change or biodiversity loss causes natural ecosystems to be less resistant to biological invasions (**sections 3.3.1**, **3.4.2**).

The biological invasion process is central to the quantitative risk assessment of invasive alien species (Leung *et al.*, 2012; **Chapter 5**, **Figure 5.1**). Nevertheless, while considerable amounts of data are being captured on the dynamics of invasive alien species across some of these biological invasion stages (Abellan *et al.*, 2016; Essl *et al.*, 2015; Gravuer *et al.*, 2008; Moodley *et al.*, 2013; Renault *et al.*, 2018; F. Ribeiro *et al.*, 2008), a full understanding of the causal factors responsible for successful introductions of invasive species remains more limited (Puth & Post, 2005). Species' traits that facilitate the introduction, establishment and spread of particular taxa (McGregor *et al.*, 2012; Moodley *et al.*, 2013; Ribeiro *et al.*, 2008) or direct drivers, such as climate change (Hulme, 2017), have been the focus of the current understanding of the transitions among different biological invasion stages.

Therefore, Chapter 3 aims to systematically[4] examine how different direct and indirect drivers of change in nature, as well as natural drivers and biodiversity loss, may influence each of the four biological invasion stages: transport, introduction, establishment and spread **(Figure 3.4)**. Specifically, each section examines the evidence for each driver within the context of the different biological invasion stages across terrestrial and aquatic biomes and for the major realms or taxonomic groups (plants, invertebrates, vertebrates and microbes; see **sections 3.1.3** and **3.6.1** for details on the search strategy and the knowledge base extracted, respectively).

4. Data management report available at https://doi.org/10.5281/zenodo.5529309

3.1.5 Attributing causality and understanding interactions among drivers

A number of studies suggest recent increases in numbers of alien species (**Chapter 2**; Seebens *et al.*, 2017) are likely augmented by increases in the rates of movement of goods and people (Essl *et al.*, 2019; Murphy & Cheesman, 2006). Due to lagged responses (time lags; or lag phase in the **Glossary**), especially towards the later stages of the biological invasion process, consequences of recent increases in transport and travel are unlikely to be fully realized at present, resulting in potentially quite substantial

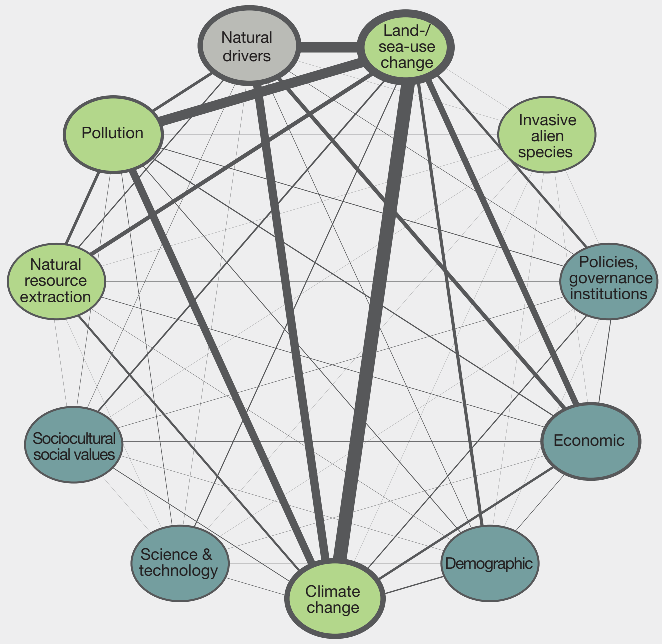


Figure 3 5 **Network diagram illustrating the extent of knowledge on indirect (blue circles), direct (green circles) anthropogenic drivers of change in nature and natural drivers (grey circle), and their interactions (lines).**

The thickness of the lines between drivers is indicative of the number of papers that jointly addressed the two linked drivers. The size of the line surrounding each circle reflects the number of papers listed by Web of Science between 2000 and 2019 generated by a topic search on a particular driver in relation to invasive alien species. Note the greater emphasis on direct drivers both individually and jointly. Note that effects of biodiversity loss on biological invasions are not included in this figure. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7861123 "invasion debts" (**Glossary**; Essl *et al.*, 2011; Rouget *et al.*, 2016; **Chapter 1**, **section 1.4.4**; **Chapter 2**, **section 2.2.1**). As a consequence of increasing rates of introduction, possibly aggravated by climate change, many historical and contemporary invasive alien species are now increasingly emerging as threats to modern agriculture and food security (Subbarao *et al.*, 2015; **Chapter 4**, **sections 4.4**, **4.5**, **4.6.2** and **4.6.3**). However, attributing such global patterns of increasing rates and impacts of invasive alien species to specific drivers, such as travel, trade, or migration, is difficult.

The drivers that directly or indirectly facilitate biological invasions are correlated and causally linked through a series of co-occurring global change trends (**section 3.1.1**). The different stages of the biological invasion process can be affected by different sets of drivers (**section 3.1.4**), and drivers can interact in complex ways to facilitate the biological invasion process (**section 3.5**). While indirect drivers of change in nature may act directly on biological invasions, both natural direct drivers and anthropogenic direct drivers of change in nature can also have indirect effects on biological invasions through their influence on other drivers or *via* feedbacks from biodiversity loss **(Figure 3.3)**. For example, climate change (direct driver of change in nature) can have a direct driving effect on land-use change e.g., through a shift to more intensive agriculture which could lead to a direct effect on biodiversity loss and thus facilitate the introduction of invasive alien species. Similarly, expanding urbanization (an indirect driver ofchange in nature) can lead to increased exploitation of hydrological resources, increased pollution, as well as habitat fragmentation (direct drivers of change in nature). All these factors may increase the extent of invasive alien species, either alone or in concert, and when in concert they may act additively or multiplicatively. Unfortunately, this complexity is rarely captured in studies of invasive alien species and research often attempts to address a single proximate cause of biological invasions rather than teasing apart multiple factors or disentangling the chain of causation from indirect to direct drivers (Hulme, 2022). The multi-driver studies that exist tend to focus on interactive effects of a few key direct drivers of change in nature, notably land-use change, pollution and climate change **(Figure 3.5)**. As a result of these complexities, the knowledge base is both limited and fragmented, and attribution of cause-effect relationships can be challenging. See **section 3.1.2** for an outline of how this challenge was tackled across the chapter, **section 3.6.2** for an overview of the resulting evidence-base, and individual driver subsections (**sections 3.2**, **3.3**, **3.4**, **3.5**) for how this was tackled or each driver.

3.2 THE ROLE OF INDIRECT DRIVERS OF CHANGE IN NATURE ON INVASIVE ALIEN SPECIES

Following previous IPBES assessments (IPBES, 2018a, 2019), the five classes of indirect drivers examined in this chapter are sociocultural drivers and social values (**section 3.2.1**), demographic drivers (**section 3.2.2**), economic drivers (**section 3.2.3**), science and technology drivers (**section 3.2.4**), and finally policies, governance and institutions drivers (**section 3.2.5**). Invasive alien species are classified as a direct driver of change in nature in the IPBES scheme (Díaz *et al.*, 2015) which implies that indirect drivers of change in nature can directly influence invasive alien species (**Figure 3.3**; **sections 3.1.3** and **3.1.4**). The specific mechanism of how these influences occur is discussed under each driver below.

3.2.1 Sociocultural drivers and social values

Sociocultural contexts, particularly social values which are created by social norms, traditions, cultural beliefs, and accepted morally by society, can exert significant pressure on decision-making regarding invasive alien species (Shackleton *et al.*, 2019; **Chapter 1**, **sections 1.5.2** and **1.5.3**). Additionally, sociocultural drivers and social values are manifested in lifestyles and consumption patterns, which act as indirect and direct drivers of change in nature and affect the transport, introduction, establishment and spread of invasive alien species **(Figure 3.6)**. Sociocultural drivers thus interact with other indirect drivers, especially demographic drivers such as changes in population density (**section 3.2.2.1**), migration (**section 3.2.2.2**) and urbanization (**section 3.2.2.4**), as people have a long history of exchanging new species and bringing them with them for ornamental, cultural and practical use. Sociocultural drivers further interact with economic drivers, such as trade (**sections 3.2.3.1**, **3.2.3.2** and **3.2.3.3**) and travel (**section 3.2.3.4**) as well as science and technology drivers, such as communication technology (**section 3.2.4.2**). Sociocultural drivers can influence the rate and magnitude of change in a number of direct drivers of change in nature, particularly related to land- and sea-use changes (**section 3.3.1**), but also species harvesting (**section 3.3.2.1**), pollution (**section 3.3.3**) and drivers related to biodiversity and ecosystem health such as unintended consequences of the intentional introduction of invasive alien species (**section 3.3.5.2**) and biodiversity loss (**section 3.4.2**).

Some alien species are associated with cultural, aesthetic or practical value (**Chapter 1**, **section 1.5.2** and **Chapter 4**,

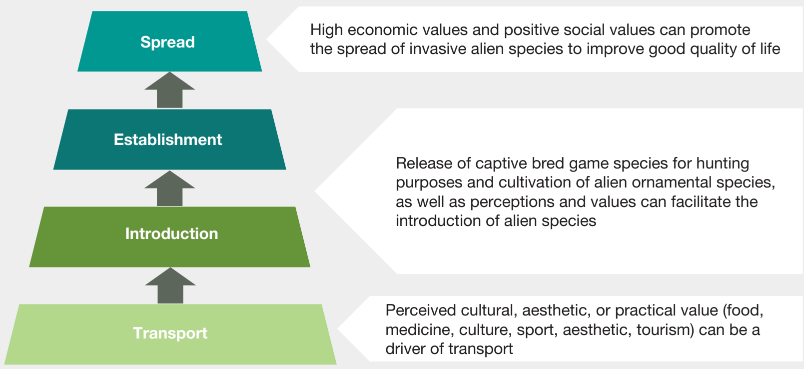


Figure 3 6 **Examples of the role of sociocultural drivers and social values in facilitating invasive alien species across stages of the biological invasion process.**

Illustration of how sociocultural drivers and social values may interact with or operate through a variety of other direct and indirect drivers of change in nature, including economic drivers, harvesting of natural resources and land- and sea-use change, to facilitate invasive alien species across the stages of the biological invasion process.

sections 4.5 and **4.6.3**), and such values can indirectly act to facilitate the introduction of these alien species. Indeed, plants that are economically valuable were shown to be 18 times more likely to become naturalized than those that are not (van Kleunen *et al.*, 2020). In Aboriginal societies in Australia, not only plants important as food and materials but also species of ritual and cultural importance have been intentionally translocated and grown for their societal and cultural benefits (Silcock, 2018). The replacement of native crayfish in Spain with two alien species intentionally introduced from North America to satisfy local tastes is a good example of the economic and social value of promoting the substitution of native species (**Glossary**) with invasive alien species (Clavero, 2016). In contrast, awareness of the adverse impacts of invasive alien species on nature, nature's contributions to people and good quality of life can lead to an increase in action by people and consequently be a driving force behind preventing the introduction of invasive alien species (McNeely, 2001; Shackleton *et al.*, 2019).

The decision to intentionally introduce an alien species or not is largely dependent on the balance between the perceived benefits of specific alien species and the perceived costs of adverse impacts. Therefore, social values have considerable influence on the judgment of whether or not to introduce an alien species (**Chapter 4**, **Box 4.2**). Estévez *et al.* (2015) reported that conflicts over invasive alien species arose primarily from differences in value systems (utilitarian, moralistic, humanistic, negativistic), rather than differences in benefit or risk perceptions between different stakeholder groups and decision-makers (**Chapter 1**, **section 1.5.2**; **Chapter 5**, **section 5.6.1.2**). According to this study, salmonids in South America, alien species of *Acacia* spp. in Africa and *Dreissena polymorpha* (zebra mussel) in Europe are examples of utilitarian vs. naturalistic value-system conflicts whereas alien mammals (example in **Box 3.2**) and trees have caused moralistic or humanistic vs. naturalistic or negativistic value conflicts in all IPBES regions (Estévez *et al.*, 2015). In another global study, Kapitza *et al.* (2019) found that the local public was more likely to focus on sociocultural benefits whereas academics focused on nativeness, and stakeholders from Africa were more likely to identify ecological benefits whereas Europeans were less likely to identify ecological and sociocultural benefits. Contextual factors, such as stakeholder role, socioeconomic status, time since the introduction occurred, and region therefore also affect the overall valuation, which again can impact behavioural choices or actions influencing biological invasions (Kapitza *et al.*, 2019; Shackleton *et al.*, 2007).

There have been many intentional introductions of invasive alien species, motivated by desires to improve specific aspects of good quality of life (**Box 3.2** and **Chapter 2**, **section 2.1.2**). Though the perception that an invasive alien species confers a benefit is not necessarily knowledge-based, it nonetheless serves as a powerful motivation for the introduction of invasive alien species usually as a result of expectations relating to increased employment, wealth, food sources, or other material gains (**Chapter 4**, **section 4.1.2**; **Chapter 5**, **section 5.6.1.2**). Meanwhile, negative impacts related to invasive alien species (whether they are intentionally or unintentionally introduced) such as threats to good quality of life, often motivates the management of biological invasions and specifically the control of invasive alien species (McNeely, 2001; Shackleton *et al.*, 2019). However, different perceptions can and often do co-exist. Specific invasive alien species considered as problematic by one social sector may provide valuable

Box 3 2 The role of hunters intentionally spreading game animals.

Introduction for hunting accounts for a large proportion of intentional introductions of invasive alien birds and mammals, both in absolute numbers and compared to introductions for biological control, pet trade and use of fur (Carpio *et al.*, 2020, 2017; Genovesi *et al.*, 2009; Hulme *et al.*, 2008). Carpio *et al.* (2017) found stocking for hunting to be a dominant source of introductions of invasive alien species. High rates of introduction and establishment can result from intensive human efforts to maintain sufficiently large and stable populations of alien species for hunting (Champagnon *et al.*, 2012, 2016). Introductions may also occur in cases where population sizes of traditionally-used native species have significantly reduced, and alien species are then introduced to supplement hunting or fishing (Carpio *et al.*, 2017; Clavero, 2016), or when alien species are introduced for the diversification of species available for hunting (Carpio *et al.*, 2017). Such efforts and considerations have resulted in large-scale introductions of a number of alien birds and mammals as game species throughout Europe, generating significant revenues through licensing fees and through creating a demand for hunting gear and services. As societal and cultural views on game species vary from being a valuable food resource *via* recreational activity to being an ecological nuisance, policy can follow suit (Duffy & Lepczyk, 2021). Alien species are still released for hunting purposes in Europe, but the rate of new species introduced has been declining over the past 10 years as the knowledge that alien species have negative effects on native ecosystems has increased (Carpio *et al.*, 2017). This increase in knowledge may have contributed to reducing the number of alien species introductions in recent decades (Fèvre *et al.*, 2006). In addition, game managers have criticized the use of alien species for hunting from an ecological perspective (Delibes-Mateos, 2015), and hunters indicate that they favour hunting wild game in biodiversity-rich landscapes rather than released individuals, and are willing to pay at least 20 times more per wild partridge *(Alectoris rufa)* hunted relative to a farm-reared bird (Delibes-Mateos *et al.*, 2014). However, hunters do not always recognize that a game species is alien (Cerri *et al.*, 2016). Furthermore, fines for the illegal importation and/or release of alien species are relatively low and the detection rate of illegal importation is low (Caudell *et al.*, 2016) compared to the economic benefit for hunters and landowners indicating that the introduction of alien species for hunting is still difficult to manage (**Chapter 5**, **Box 5.6**).

Figure 3 7 ***Phasianus colchicus* (common pheasant) killed by a recreational shoot.**

Phasianus colchicus are native to Asia and parts of Europe (Balkans and northern Caucasus) and have been introduced as game birds throughout the world, including Europe, North America, Hawaii, Japan, Australia and New Zealand. In the United Kingdom, pheasants were introduced in the eleventh century and became a popular game bird in the nineteenth century, being widely bred and released for recreational use. The current breeding population in the United Kingdom has 2.3 million female birds (RSPB, 2021). Photo credit: MykolaMoriev, Shutterstock – Copyright.

contributions to people, cultural benefits, or other intrinsic values to another (**Chapter 1**, **section 1.5.2**; McNeely, 2001; Schlaepfer *et al.*, 2011). For example, in poor rural communities in Madagascar, the introduced *Procambarus virginalis* (Marmorkrebs), while acknowledged to be detrimental to rice farming and fishing, is also valued as a cheap and widely accessible protein source for food and feed, and the perception of overall benefit relative to costs is considered high by people not directly involved in fishing or farming and by communities with a long history of crayfish invasion (Andriantsoa *et al.*, 2020). *Opuntia ficus-indica* (prickly pear), an invasive alien cactus, has high economic value to rural communities in South Africa, where it is used for stock fences or as fresh fruit, and as such is considered positively by farmers, which has consequently affected its establishment and spread (Kapitza *et al.*, 2019; Shackleton *et al.*, 2007). Other examples include invasive alien species introduced as game animals **(Box 3.2)** or for recreational fishing.

3.2.2 Demographic drivers

Demographic drivers, including human population growth and movement, are fundamental factors behind many drivers that directly facilitate biological invasions. This section summarizes the evidence for the influence of four main demographic drivers of change in nature: 1) changes in human population density; 2) human migration; 3) international crises, such as armed conflict and emergency relief; and 4) urbanization **(Figure 3.8)**.

Demographic drivers of change in nature interact with other indirect drivers, especially economic drivers, such as trade (**sections 3.2.3.1** to **3.2.3.3**) and travel (**section 3.2.3.4**) and science and technology drivers, such as breeding and genomic technologies (**section 3.2.4.3**). Demographic drivers operate by influencing the rate and magnitude of change in a number of direct drivers, most obviously those related to land- and sea-use change (**section 3.3.1**), but also other direct drivers such as species harvesting (**section 3.3.2.1**), water extraction (**section 3.3.2.2**), pollution (**section 3.3.3**), climate change (**section 3.3.4**) and drivers related to biodiversity and ecosystem health such as unintended consequences of the intentional introduction of invasive alien species (**section 3.3.5.2**) and biodiversity loss (**section 3.4.2**).

3.2.2.1 Regional and national changes in human population density

The world's population has doubled over the last 50 years (IPBES, 2019) and is expected to reach 8.5 billion people in 2030, of which approximately 60 per cent (about 5 billion) will reside in urban areas (**section 3.2.2.4**; United Nations *et al.*, 2019). Coastal areas are experiencing faster growth rates and 51 per cent of the world's population will live within 100km of the coast by 2030 (Kummu *et al.*, 2016). Approximately 75 per cent of the two billion people to be added to the global population by 2050 will live in sub-Saharan Africa (about 50 per cent) and Central and Southern Asia (about 25 per cent) (United Nations *et al.*, 2019). Regions with high human population densities are often associated with high rates of species introductions and establishment of alien species (Pyšek *et al.*, 2020), and have been associated with both intentional and unintentional transport of species to locations outside of their native ranges (Hulme, 2009; Levine & D'Antonio, 2003). Human population density growth enhances regional trade (**section 3.2.3.1**; United Nations *et al.*, 2019), intensifies

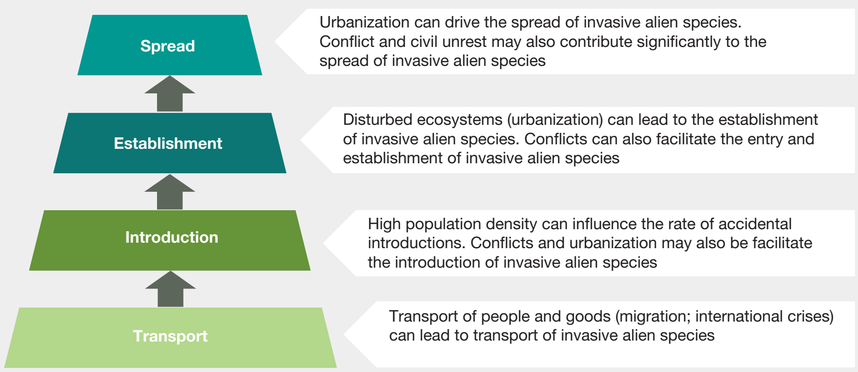


Figure 3 8 **Examples of roles of demographic drivers in facilitating invasive alien species across stages of the biological invasion process.**

Illustration of how demographic factors such as urbanization, international crises and movement of people, directly or *via* other drivers such as land-use change, can facilitate invasive alien species across the stages of the biological invasion process.

urbanization (**section 3.2.2.4**), and increases pressures from a suite of land-use related factors, including nature-based industries (**section 3.3.1.1**), and is associated with the loss, fragmentation and degradation of natural ecosystems (**sections 3.3.1.2** to **3.3.1.5**; IPBES, 2019). These are all factors known to promote alien species in terrestrial (Pyšek *et al.*, 2020) and marine environments (C. C. Murray *et al.*, 2014) across multiple taxonomic groups (Bellard *et al.*, 2016). Evidence from several regional and global studies (Dawson *et al.*, 2017; Essl *et al.*, 2019) shows that alien species richness is positively associated with human population density with human population density-related processes acting on different stages of the biological invasion process (Pyšek *et al.*, 2010). In a global study of a wide taxonomic range of established alien species (**Glossary**), human population density was shown to have the strongest influence on fish, plants and spiders whereas weaker but positive relationships were found for ants, birds, mammals and reptiles (Dawson *et al.*, 2017). In Europe, human population density is positively associated with increased alien species richness for a wide range of plant and animal groups, with highest alien species richness values occurring in regions with more than 91.1 inhabitants/km^2 and the lowest values in regions with fewer than 8.5 inhabitants/km^2 (Pyšek *et al.*, 2010). At the national scale, a comprehensive national alien species assessment in Norway, covering all multicellular organisms, found that for all taxonomic groups considered (terrestrial and aquatic plants, invertebrates, fungi and vertebrates) alien species richness was positively correlated with human population density (Sandvik *et al.*, 2019). Similarly in the United Kingdom, human population density was a good predictor of freshwater fish introductions (Copp *et al.*, 2010). In Brazil, Fonseca *et al.* (2019) showed that human population density influenced the rate of unintentional introductions, resulting in high records of alien amphibians and reptiles in densely-populated areas. At more local scales, evidence shows that increased human population density in surrounding areas is a significant predictor of alien species richness for plants within national parks in the United Stated of America (McKinney, 2002) and for multiple alien taxa (including birds, mammals, vertebrates and plants) in South Africa's Kruger National Park (Spear *et al.*, 2013). The number of visitors (McKinney, 2002) or occupants (Foxcroft *et al.*, 2008) within a national park is positively correlated with alien species richness. A case study on urban wetlands further highlights that alien species richness is correlated with human population density, however found that alien herbs, shrubs and trees all respond differently to human pressures (Ehrenfeld, 2008).

Human population density can be used as a proxy to better understand the role of various human activities across stages of the biological invasion process, and has been shown to facilitate both introduction (Gallardo & Aldridge, 2013; Pyšek *et al.*, 2010) and establishment (Dawson *et al.*, 2017). This may be related to human population density acting as a proxy for propagule pressure (**Glossary**) and the intensity of anthropogenic disturbance (**section 3.3.1**), two mechanisms known to facilitate the introduction and establishment of alien species, respectively (Gallardo & Aldridge, 2013; Roura-Pascual *et al.*, 2011). For example, in Europe, the introduction of alien mammals was significantly correlated with human population density whereas establishment success was not (Jeschke & Genovesi, 2011). At the global scale, other socio-economic factors, such as per capita GDP and proportion of agricultural land, appear to be more important predictors of relative invasive alien species richness than population density across both islands and mainland regions (Essl *et al.*, 2019; Westphal *et al.*, 2008). Essl *et al.* (2019) show that human population density had a greater influence on absolute alien species richness in mainland regions compared to islands, and this pattern was more pertinent for established alien species than for the subset of alien species that were invasive. This illustrates that while population density is correlated with invasive alien species dynamics, the relationship is complex so that countries that have high rates of population growth are not necessarily those with high rates of introduction of invasive alien species.

The review of the literature for this chapter (**section 3.6.1**)[5] highlighted that the majority of the evidence for human population density as a driver that facilitates biological invasions can be found in the terrestrial realm, followed by the freshwater realm, with few marine examples to draw from despite the large concentration of human populations living near to the coast. The IPBES regions of Oceania and Asia-Pacific were the least well studied, with Europe and the Americas having the greatest focus. Despite the other regions (e.g., Africa) being included in global studies, they have relatively few examples to draw from and examples are often from a small selection of countries (e.g., South Africa). Dawson *et al.* (2017) provide a global synthesis of the taxa, however microbes and invertebrates remain poorly studied.

3.2.2.2 Human migration

While the term migrant has specific definitions, Chapter 3 specifically focuses on people moving away from their place of usual residence to take up residence in another country. The rate of migration is increasing: in 2019, 3.5 per cent of the global population (272 million people) were living in a country other than their country of birth, compared with 2.8 per cent in 2000 and 2.4 per cent 1980 (International Organization for Migration, 2019; Vidal *et al.*, 2018). Migrating humans act as direct dispersal vectors (**Glossary**) in the transport and spread of plants, animals and microbes, either unintentionally in the case of pests and diseases or

5. Data management report available at https://doi.org/10.5281/zenodo.5529309

intentionally in the case of pets, livestock, ornamentals, or crops. Sociocultural drivers and social values (**section 3.2.1**) are important factors behind many of these intentional introductions. Human migration thus operates through and in synergy with other indirect drivers of change in nature such as changes in travel, trade and transport (**sections 3.2.3.1** to **3.2.3.4**), urbanization and/or abandonment of land (**section 2.3.3.4** and **3.3.1.5.1**) and population changes, armed conflict and emergency relief (**sections 3.2.2.1** and **3.2.2.3**).

Generally, broad-scale analyses of the spread and distribution of alien species find links between the rate and origins of introductions of new species and human migration history. For example, early introductions of invasive alien plants in Brazil and Australia can be linked to waves of European migration (Phillips *et al.*, 2010; Zenni, 2014), patterns of early bird introductions worldwide spatially and temporally tracked the expansion of European (and especially British) colonialism (Dyer *et al.*, 2017). Patterns of ant invasion dynamics globally bear clear imprints of human demographic patterns including an early wave of biological invasions (1850-1910) coinciding with a period of high human migration (Bertelsmeier *et al.*, 2017). As a more recent example, the number of insect invasions in Europe increased steeply in response to political changes that allowed increased movement of people and goods in Europe after the fall of the Iron Curtain in 1989, and also increased following the expansion and integration of the European Union (Roques *et al.*, 2016). Similarly in line with geopolitical and economic trends, vertebrate introductions from Europe to the United States of America peaked in the nineteenth century paralleling high rates of human migration in the same direction, while alien vertebrate introductions in the opposite direction (United States to Europe) are at their highest now (Jeschke & Strayer, 2005).

Migration can also drive introductions and spread of alien species within regions, for example, immigrants to South Africa from other countries in the region have brought with them their own medicinal plants and have created a market for them (Faulkner *et al.*, 2020). A parallel line of evidence for the role of historic human migration on alien species' distributions comes from intraspecific genetic patterns in alien species. Several studies reveal close congruence with historical large-scale human migration, including for human diseases carried directly by humans or by vectors associated with humans (e.g., Conn *et al.*, 2002), pests (e.g., Puckett & Munshi-South, 2019) and even parasites of pests (e.g., Aketarawong *et al.*, 2015; United Nations Department of Economic and Social Affairs, 2019). Accordingly, political or other barriers to human migration can impede rates of spread of alien species, as is seen in the spread of alien insects across Europe, which appears to have been hampered by the political East-West barrier during the Cold War, as rates of spread were four times higher after 1989 compared to the 1950-1989 period (Roques *et al.*, 2016).

While human migration is increasing globally (United Nations Department of Economic and Social Affairs, Population Division, 2020), other movements of people and goods around the globe resulting from trade and direct use of alien species in nature-based industries (**sections 3.2.3.1**, **3.3.1.1**) and travel and tourism (**section 3.2.3.4**) are increasing even more rapidly (UNWTO, 2021). The relative importance of human migration *per se* in the introduction of invasive alien species is therefore likely to be decreasing. In line with this, recent global analyses reveal only weak influence of human migration on recent patterns in the rate of alien species' introductions, and also weak influences of human migration rates on variation in biological invasions among taxonomic groups and between geographic regions (Seebens *et al.*, 2015). However, human migration is predicted to rise as climate change displaces people from drought-, flood- or storm-hit regions (Rigaud *et al.*, 2018), indicating that human migrations, possibly in interaction with climate change, land-use change or natural drivers, could contribute to increased rates of introduction of invasive alien species in the future. Pressure from invasive alien species could be expected to be highest in countries with the highest inward migration: currently United States, Germany, Saudi Arabia, Russian Federation and the United Kingdom (United Nations Department of Economic and Social Affairs, Population Division, 2020).

While the review of the literature on human migration as a driver facilitating biological invasions undertaken in Chapter 3 is limited in extent, authors considered evidence from plants, vertebrates, invertebrates and microorganisms, and from all IPBES regions, with evidence dating back to colonial times (**Chapter 2**, **section 2.2.1**). As such this section broadly covers relevant variability in terms of geography, taxonomy and realms and time. The literature on migration as a driver facilitating biological invasions is focused on the transport and especially introduction of alien species, with less evidence from the latter stages of the biological invasion process.

3.2.2.3 International crises: armed conflict and emergency relief

International crises, specifically armed conflicts and humanitarian emergency relief and development assistance operations can be powerful indirect drivers of change in nature that may directly facilitate the transport, introduction, establishment and spread of invasive alien species (**Chapter 6**). By 2020, the global number of refugees and asylum seekers was approximately 25 million people (UNHCR, 2020). Both crises and aid can affect biological invasions through abrupt and substantial changes in travel, trade and transport (**sections 3.2.3.1** to **3.2.3.4**), and through substantial and rapid human population movements and changes (**sections 3.2.2.1** and **3.2.2.2**). These trade, transport and population changes affect biological invasions through influencing, broadly, the movement of goods and deployment of infrastructure, and the transport and movement of humans and their luggage, all of which can act as direct dispersal vectors (assisting the uptake and introduction of alien species both intentionally or unintentionally; **section 3.3.1.1**). Crises and aid can also lead to changes in nature through increasing or decreasing the intensity of land- and sea-use (**section 3.3.1.1**), which may again affect biological invasions (e.g., fragmenting landscapes, creating corridors, deploying infrastructure, leading to land-use abandonment, degrading habitats, or changing disturbance regimes; **sections 3.3.1.2** to **3.3.1.6**).

Conflict and civil unrest may contribute significantly to the introduction and spread of invasive alien species through several mechanisms: (i) civil unrest or war can lead to the breakdown of phytosanitary and animal health control and management, and the loss of supply lines for materials as well as to the displacement of large numbers of people; (ii) areas where there is civil unrest or war may be more vulnerable to the introduction of invasive alien species because of the lack of inspections and border controls, facilitating unregulated movement as well as deliberate smuggling of people and their belongings, and also because of the increased movement of military personnel and refugees; (iii) inflows of food aid may also be contaminated with alien species; and (iv) difficulties in obtaining access to border areas because of landmines and other hazards impedes border control (FAO, 2001; Moore, 2005; Murphy & Cheesman, 2006).

War entails transportation of people and goods, deployment of heavy machinery, disturbance of habitats, creation of bare ground, and in some instances intentional introductions of alien species (food supply etc.; Fosberg, 1957). Military transport, equipment and supplies, often covered with dirt or mud from the field, are effective means of dispersal for many alien species (Cofrancesco Jr *et al.*, 2007; Dalsimer, 2002). A number of introductions have been linked to movement of troops and military equipment during the Second World War: *Rattus rattus* (black rat) were introduced to the Midway Islands by navy ships; a desert shrub, *Peganum harmala* (African rue) was introduced inadvertently into New Mexico and Texas *via* airfields; *Tribulus terrestris* (puncture vine) and the agricultural pests *Striga asiatica* (witch weed) and *Globodera rostochiensis* (yellow potato cyst nematode) are believed to have entered North America on returning military equipment; and *Boiga irregularis* (brown tree snake), native to New Guinea, was unintentionally introduced to the island of Guam most likely in military shipments of fruit (Cox, 1999). A root rot of pine trees, *Heterobasidion annosum* (root rot), was inadvertently introduced into Italy by American troops during World War II where it has resulted in an unprecedented mortality rate of *Pinus pinea* (Italian stone pine; Pilcher, 2004). More generally, an increase in marine invasive alien species was observed at Pearl Harbor following World War I and II (Coles *et al.*, 1999). More localized military operations have also led to biological invasions. The introduction of *Diabrotica virgifera* (western corn rootworm) in Serbia in the 1990s was associated with incoming military transport from the United States (EPPO, 1996), and has rapidly become a widespread (**Glossary**) threat to European corn production (Bažok *et al.*, 2021). Habitat disturbance caused by military activity may also facilitate invasive alien species. In Poland, bomb craters were found to have higher numbers of invasive alien plants compared to the surrounding landscape (Krawczyk *et al.*, 2019). Military training activities resulting in soil disturbance facilitated the spread of *Imperata cylindrica* (cogon grass) in military camps in the United States (Yager *et al.*, 2009). Again in the United States, tank traffic activity facilitated invasive alien species in prairie grasslands (Wilson, 1988).

War also facilitates the movement of humans, who may themselves become vectors of alien species including pathogens. For example, the global spread of the Spanish Flu post-World War I was attributed to movement of troops (Neill & Arim, 2011) and a 2010 cholera outbreak in Haiti was attributed to incoming United Nations peacekeeping troops from Nepal (Frerichs *et al.*, 2012). Not all war and crisis-related introductions are unintentional. *Mikania micrantha* (bitter vine) is reported to have been introduced to northeast India to camouflage air strips built by the Allied Forces during World War II to impede the advancing Japanese forces (Kohli *et al.*, 2011; Randerson, 2003). More unique links between armed conflicts and biological invasions also exist, for example, attempts to rectify war damages through replanting activities and making use of invasive alien species in these efforts, i.e., the planting of *Cynodon dactylon* (Bermuda grass) or revegetation of denuded Pacific islands during World War II (Fosberg, 1957). War can also hamper biological invasions, as exemplified by reductions in the rates of global spread of alien ant species due to decreased global trade in both World Wars I and II (Bertelsmeier *et al.*, 2017).

Emergency relief, reconstruction efforts and humanitarian aid after armed conflicts and disasters may also contribute to the introduction and spread of invasive alien species. For example, *Iguana iguana* (iguana), *Osteopilus septentrionalis* (Cuban treefrog) and *Scinax x-signatus* (Venezuela snouted treefrog) were introduced to Dominica, West Indies, *via* emergency relief shipping containers (van den Burg *et al.*, 2019). *Parthenium hysterophorus* (parthenium weed), originally from Mesoamerica, has become invasive in India, where its seeds arrived in grain shipments. It was then spread to Sri Lanka *via* peacekeeping efforts (Kohli *et al.*, 2006; Pallewatta *et al.*, 2003). Aid shipments also resulted in its introduction to Ethiopia (Wittenberg & Cock, 2003).

Such cases have led to local concern when receiving humanitarian aid shipments. For example, due to the highly invasive nature of *Sorghum halepense* (Johnson grass), American Samoa refused the offer of assistance from the Australian International Assistance Program (Tuinoula, 2003).

As illustrated in this section, the scientific and especially grey literature[6] provide a range of examples of how international crises, specifically armed conflicts and emergency relief, may act as a driver facilitating biological invasions both through intentional introductions for various purposes and unintentional introductions through contaminants and stowaways. Authors found evidence from plants, vertebrates, invertebrates and microorganisms; from terrestrial, aquatic and marine systems; and from all IPBES regions. The literature on international crises and aid as a driver facilitating biological invasions covers all stages of the biological invasion process, especially focusing on the introduction and spread phases, the latter often from assessments of impact (**Chapter 4**).

3.2.2.4 Urbanization

Urbanization, the increase in the proportion of a population living in urban areas, results in a large number of people becoming permanently concentrated in relatively small areas, forming cities (IPBES, 2022c). By 2018 approximately 55 per cent of the world's population resided in urban areas, and it is expected that this will exceed 60 per cent by 2030 (United Nations, Department of Economic and Social Affairs, Population Division, 2019). As the global human population increases, the patchwork of urban sprawl and modified environments is increasingly dominating landscapes. This accelerated urban growth has contributed to the extensive fragmentation, reduction and degradation of natural ecosystems worldwide (IPBES, 2019) facilitating the establishment and spread of invasive alien species in urbanized areas (**sections 3.3.1.2** to **3.3.1.5**). Along with the increase in human population density in cities (**section 3.2.2.1**), the volume, frequency and range of movement of people and goods also increases, as does trade (**sections 3.2.3.1** to **3.2.3.4**). The movement in people and goods operates at many scales, from local, through national and regional scales, to global networks, facilitating transport of invasive alien species at all scales.

In a global review of invasive alien plants, vertebrates and invertebrates on islands (749 alien species in total), urban areas had consistently higher abundances of alien species compared to natural ecosystems (Sánchez-Ortiz *et al.*, 2020). Urban areas are centres of transport and travel, facilitating breakdown of biogeographic barriers and high rates of introduction of invasive alien species into urban habitats (Banks *et al.*, 2015). Accordingly, the richness of alien plants in urbanized areas is related to factors such as length of railroads and roads, and the size of the urbanized area (Kühn *et al.*, 2017). However, pathways vary across taxonomic groups, with escape from containment in homes or gardens being the most likely source of invasive alien plants and vertebrates in urban areas, whereas invertebrates are likely to arrive as stowaways or contaminants in transported goods (Padayachee *et al.*, 2017). Many invasive alien species have generalist or opportunistic traits, and urban areas may provide suitable environments and novel opportunities for their establishment and spread. In the case of birds, for example, urban environments offer opportunities for species with flexible foraging strategies to adopt novel food sources; favouring invasive alien birds that tend to be more flexible in their behavioural traits relative to native species (Griffin *et al.*, 2017). Similarly, for plants, the increased disturbance (**section 3.3.1**), pollution and nutrient availability (**section 3.3.3**), and climate warming (**section 3.3.4**) associated with urbanization generate opportunities for alien species, many of which are habitat generalists and/or disturbance and high-nutrient habitat specialists. The number of invasive alien species in urban areas is predicted to increase further due to an increase in propagule pressure and opportunities for the spread and establishment associated with increased global trade, intentional release of alien species, land-use intensification, urbanization and climate change (Dawson *et al.*, 2017).

In some cases, urban areas are a focus for the spread into the wider environment and may have major implications for Indigenous Peoples and local communities, as in the case of Montréal, where wetlands are invaded by invasive alien species due to clearing and filling activities occurring around Indigenous lands (IPBES, 2022b). Accordingly, many studies have found a positive association between the number of invasive alien species within a location and the percentage of urban land in the surrounding landscape (Vilà & Ibáñez, 2011). Similarly, road density, frequency of road use and road improvement increases diversity of alien species in adjacent ecosystems (Vilà & Ibáñez, 2011).

Urbanization can also be a driver for aquatic invasive alien species. Out of 891 species listed in the Global Invasive Species Database (GISD; GISD, 2021), 277 (31 per cent) are associated with urban areas, 395 (44 per cent) are associated with inland waters (wetlands, lakes, or water courses), and 147 (16 per cent) are associated with both urban areas and inland waters (**Chapter 2**, **section 2.5.5.1**). Urbanization provides two means for enhanced invasions into wetlands. First, large numbers of species are imported (intentionally or unintentionally) into urban areas, creating high propagule pressures, and second, urbanization causes disturbance of existing ecosystems (Hassall, 2014). For example, deployment of infrastructure (**section 3.3.1.4**) such as stormwater ponds may harbour the invasive

6. Data management report available at https://doi.org/10.5281/zenodo.5529309

alien *Anaxyrus fowleri* (Fowler's toad) and construction may facilitate the dispersal of this invasive alien species. Urbanization may facilitate biological invasion in or around aquatic environments through modification of channels and banks (**section 3.3.1.4**), disturbance from traffic, presence of pet animals (**section 3.3.5**), dumping of rubbish (**section 3.3.3**), and reductions in permeability of surrounding land (Hassall, 2014; **section 3.3.1.6**).

Urbanization also plays a role in the relative distribution and abundance of both native and alien species in marine environments. Deployment of marine infrastructure (**section 3.3.1.4**) is an important direct driver, and large coastal and marine areas of Europe, North America, Asia and Australia are nowadays covered by sea walls, dikes, breakwaters, groynes, jetties, pilings, bridges, artificial reefs, offshore platforms and energy installations, which are linked to urban areas. A study carried out by Airoldi *et al.* (2015) found that marine infrastructures along sandy shores disproportionally favour alien over native hard bottom species, affecting alien species' spread at regional scales.

3.2.3 Economic drivers

Alien species are dispersed globally and regionally both intentionally and unintentionally through trade and commerce (**sections 3.2.3.1** to **3.2.3.3**) and by travellers and tourists (**section 3.2.3.4**). While the causal relationships are complex, the resulting pattern can be relatively simple and predictable. The number of alien species found in a country often correlates with per capita GDP (Dawson *et al.*, 2017; Essl *et al.*, 2011) reflecting the intensity of international trade which is a major conduit for the introduction of alien species (Hulme, 2009).

Economic drivers impact and interact with other indirect drivers of change in nature, especially demographic drivers, such as population density (**section 3.2.2.1**) and urbanization (**section 3.2.2.4**). Economic drivers operate by influencing the rate and magnitude of change in the majority of the direct drivers of change in nature, including those related to land- and sea-use change (**section 3.3.1**), direct exploitation of natural resources (**section 3.3.2**), pollution (**section 3.3.3**), climate change (**section 3.3.4**), and drivers related to the intentional introduction of invasive alien species and associated unintended consequences (**section 3.3.5.2**) and biodiversity loss (**section 3.4.2**). Section 3.2.3 describes evidence for links between specific economic drivers and invasive alien species **(Figure 3.9)** and makes reference to other indirect and direct drivers when relevant. Mechanistic links between the ensuing direct drivers and invasive alien species are discussed in **section 3.3**.

3.2.3.1 International trade and global commerce

International trade (whether legal or illegal) in commodities (e.g., minerals, petrochemical products, agricultural products, machinery and electronic goods, plants and wildlife) is an important route through which invasive alien species are introduced into new regions (Hulme, 2021b). International trade has grown dramatically since 1950 (Hulme, 2009, 2021b), and the quarterly world trade volume more than doubled from 2005 (2.5 trillion US dollars (US$)) to 2019 (over US$6 trillion; WTO, 2021), so that few nations in the world are not linked to others through trade. In many ways, trade is a universal driver facilitating biological invasions across contexts, playing a role in the introduction of aquatic and terrestrial taxa

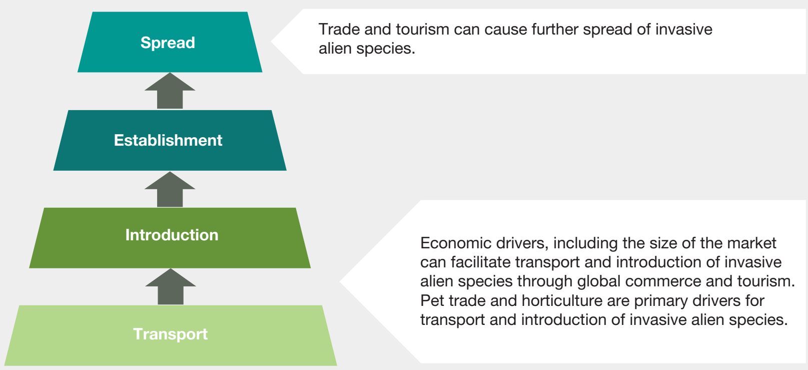


Figure 3 9 **Examples of the role of economic drivers in facilitating invasive alien species across stages of the biological invasion process.**

Economic factors such as size of markets and trade and use of specific invasive alien organisms can facilitate their transport and introduction, whereas trade and tourism can facilitate the further spread of invasive alien species within regions.

across the world. The demand for increased international trade has led to a major shift in the magnitude and reach of international shipping, and to the development of ports and deep-water harbours, inter-regional canals and global air freight (Hulme, 2009a; **section 3.3.1.3**, **Box 3.7**; **section 3.3.1.4**). Government officials at international borders regularly intercept invasive alien species associated with a wide range of imported commodities and transport vectors (Bacon *et al.*, 2012; Caley *et al.*, 2015; McCullough *et al.*, 2006; Work *et al.*, 2005). Clearly, the more locations at which international commodities first arrive in a country (airports, seaports, land-borders), the greater the likelihood that invasive alien species will succeed in finding a suitable environment (**Chapter 1**, **section 1.4.1**; **Chapter 2**, **section 2.1.2**).

The direct effects of trade have largely been quantified using relationships between imports and the number of alien species in a region or patterns in the global spread of species linked to shipping and air traffic networks (Hulme, 2021b). Alien species may themselves be the imported commodity (e.g., aquarium, ornamental, pet, crop, or pollinator species; **Box 3.3**), or a contaminant of a commodity (e.g., plant pathogens on a host plant, seeds trapped in wool fleeces, or insects in grain shipments), or be associated with a transport vector as a stowaway (e.g., hull fouling or ballast water organisms associated with marine transport). For example, invasive alien species of ornamental fish (Padilla & Williams, 2004; Hixon *et al.*, 2016), plants (Hulme *et al.*, 2018) and insects **(Box 3.3)** are traded globally as a commodity. The international pet trade is recognized as a primary driver for the introduction of invasive alien animals (Hulme, 2015a; Maceda-Veiga *et al.*, 2013). The introduction of *Aedes albopictus* (Asian tiger mosquito) is well known as a contaminant of imported used tyres (Benedict *et al.*, 2007), and large numbers of alien vertebrate and invertebrate species have been introduced as stowaways in ballast water (Molnar *et al.*, 2008). There is also evidence that illegal wildlife trade also runs the risk of introducing some invasive alien species into new regions (García-Díaz *et al.*, 2016). Furthermore, international trade has been a driver for the initial construction and, more recently, expansion of shipping canals (e.g., Suez, Panama) that by linking previously separate marine regions have facilitated the spread of invasive alien species between seas and oceans (Golani, 2021; Hulme, 2015b; **section 3.3.1.3**, **Box 3.7**). In addition to the transport and introduction of invasive alien species across international borders, commerce can also facilitate the establishment and spread of alien species within a region. For example, the size of the national market for ornamental plants (Dehnen-Schmutz *et al.*, 2007) and freshwater crayfish (Chucholl, 2013) is a strong driver that increases the likelihood of species becoming established in the wild. Such trends are likely to be exacerbated by the growth in e-commerce (**Glossary**) of alien species (Humair *et al.*, 2015).

Not all alien species introductions are associated with a specific commodity; some alien species may enter a region on vectors rather than commodities, that is they are associated with the mode of transport. Alien species introduced in ballast water are more likely to reflect the volume, frequency, age and origin of marine vessels than the specific commodities carried by shipping (Hulme, 2021b). The network of global ship movements and the estimated volume of ballast water discharges in ports worldwide have been used successfully to identify the major source regions for invasive alien species in several maritime ecoregions (Seebens *et al.*, 2016). However, there has been a five-fold increase over the past 30 years in the number of shipping containers carrying international trade but, despite the risk containers pose, there have been no studies to date attempting to relate contemporary risk of invasive alien species to variation in the number of containers imported or indeed their global itineraries (Hulme, 2021b).

There is often a strong correlation between the number of alien species in a country and the value of commodity imports, supporting the view that international trade is a key driver in the introduction of invasive alien species (Levine & D'Antonio, 2003; Santini *et al.*, 2013; Seebens *et al.*, 2015; Westphal *et al.*, 2008). Such relationships are often nonlinear, suggesting that the effect of imports on alien species numbers becomes less strong once a certain threshold is reached, and can vary in strength quite markedly depending on the taxonomic group examined (Hulme, 2021b). Coarse correlations with the value of all commodity imports often mask important detail regarding the relationship between trade and the multiple pathways of introduction of alien species (Hulme *et al.*, 2008). Even within a single pathway there may be subtle differences in the risk posed by particular commodities, as in the case of invasive alien insects that are more likely to enter the United States as contaminants of commodities transported in refrigerated rather than unrefrigerated cargo (Work *et al.*, 2005).

Knowledge that the likelihood of the introduction of alien species varies by trading partner has led to studies examining wider bilateral trade relationships more thoroughly (Hulme, 2021b). As a result, data on the magnitude of bilateral trade between regions is often used to estimate the scale of future biological invasions and has, to date, pointed to a significant increase in risk over the next decades (Bradley *et al.*, 2012; Seebens *et al.*, 2015). These risks differ by global region, with some evidence suggesting there are greater risks for developing countries (Seebens *et al.*, 2015). Given the strong link between international trade and biological invasions, the global economic slowdown that was initiated by the 2008 financial crisis (Constantinescu *et al.*, 2016) might be expected to have reduced the rate of alien species establishment however, evidence suggests rates of establishment are likely to lag behind economic drivers by as much as two decades (Seebens *et al.*, 2015). Thus, for the foreseeable future, rates of alien species introductions through trade will continue to increase. As a consequence, future trends in international trade, including e-commerce, new trade routes, and major infrastructure developments, will lead to pressure on national borders that may soon outstrip the resources available for intervention (**Chapter 6**, **section 6.3.1.4**).

Box 3 3 **Trade of bumblebee colonies for crop pollination as a driver that facilitates the introduction of invasive alien species.**

Many pollinators and flower visitors from various insect orders and families have been introduced and established out of their native ranges (Bartomeus *et al.*, 2013; Goulson, 2003, **Chapter 1**, **Box 1.11**). Unintentional transportation with their host materials accounted for the establishment of cavity-nesting bees (e.g., *Anthidium manicatum* (wool carder bee)), whereas crop pollination motivated the intentional transportation and introduction of *Apis* (honey bees) and *Bombus* (bumble bees) (Gibbs & Sheffield, 2009; Goulson, 2003; Schweiger *et al.*, 2010). While different subspecies of *Apis mellifera* (European honeybee), native to Europe and Africa, have been managed at least since 2450 B.C., (Crane, 1999) and introduced in all continents (except Antarctica) where they were not native, the introduction of *Bombus* spp. (bumblebee) colonies is relatively recent (Osterman *et al.*, 2021). Bumblebees live in colonial nests and can buzz pollinate (whereby bees use vibrations to extract pollen from flowers, incidentally, fertilizing them), making them suitable pollinators for a wide range of crops, in particular those grown in greenhouses. The rearing of bumblebee colonies of European species *Bombus terrestris* started in the 1980s and in a few years triggered a massive trade of colonies within and beyond its native range **(Figure 3.10)**. This species has invaded many countries in which it has been intentionally introduced (e.g., Japan, New Zealand, Chile) expanding its range even to countries were introduction was not allowed, as is the case of Argentina (Aizen *et al.*, 2019). In South America, *Bombus terrestris* has spread across Chile (Montalva *et al.*, 2011) from the Atacama Desert to the southernmost islands south of the Tierra del Fuego Archipelago and to South West Argentina (Morales *et al.*, 2013). In this region *Bombus terrestris* achieves unusually high abundance and dominance of local pollinator communities (Aizen *et al.*, 2014; Morales *et al.*, 2017). Moreover, the indroduction of *Bombus terrestris* has facilitated the co-introduction of novel pathogens (Arbetman *et al.*, 2013; **section 3.3.5.1**).

Figure 3 10 **Growers can purchase bees in a box that will fly from flower to flower, distributing pollen among the plants.**

Many pollinators and flower visitors from various insect orders and families have been introduced and established out of their native ranges. Photo credit: jpr03, Adobe Stock – Copyright.

3.2.3.2 Trade in plants for horticulture, agriculture, ornamental use and nurseries

Globally, 67 per cent of alien terrestrial plants have been introduced intentionally through horticultural (46 per cent) or agricultural (21 per cent) pathways (Turbelin *et al.*, 2017). Ornamental use of plants is a dominant driver facilitating the introduction of invasive alien species that has also been increasing in recent years (Dodd *et al.*, 2015; Faulkner *et al.*, 2016; Hulme *et al.*, 2018; Lambdon *et al.*, 2008; Lehan *et al.*, 2013; Mayer *et al.*, 2017). Accordingly, there is an increasing rate of escapes from ornamental cultivation into the wild (Haeuser *et al.*, 2018; van Kleunen *et al.*, 2018), with at least 75 per cent of the global established alien flora grown in domestic gardens, and 95 per cent grown in botanical gardens (van Kleunen *et al.*, 2018). In some countries (e.g., United Kingdom, New Zealand) the number of species in cultivation exceed the number of native species in the wild (Armitage *et al.*, 2016; Gaddum, 1999; Hulme, 2020), and in some, such as the United States, alien species form the bulk of nursery stock (Brzuszek & Harkess, 2009). Unintentional introduction through seed contaminants associated with the intentional introduction of ornamental plants is regarded as the second most important source of invasive alien plants in the United States and has become increasingly important in recent years (Lehan *et al.*, 2013). Horticulture was also the primary pathway (**Glossary**) of alien introductions in Puerto Rico and the Virgin Islands (Rojas-Sandoval & Acevedo-Rodríguez, 2015). In the West Indies, 75 per cent of all invasive alien plants have escaped from cultivation, and 51 per cent of all introductions are through the ornamental pathway (Rojas-Sandoval *et al.*, 2017).

Ornamental and agricultural use is also a major source of aquatic plant invasions. In the People's Republic of China, more than 50 alien freshwater aquatic plants have been introduced for ornamental, landscaping, water purification, forage and other purposes, around 20 per cent of which are now considered invasive (Wu & Ding, 2019). In Europe and the Mediterranean region, large numbers of ornamental aquatic alien plants are unintentionally released from aquaria, dumped from water gardens, or escaping from managed environments, a number of which have become invasive (Brundu, 2015). Many ornamental aquatic alien species may become widely distributed, for example *Pontederia crassipes* (water hyacinth) which was introduced from South America to botanic gardens and ornamental ponds around the world from the nineteenth century onwards is now found across more than 50 countries on five continents (Sharma *et al.*, 2015; **section 3.5.2**, **Box 3.12**).

3.2.3.3 Trade in terrestrial pet animals

Pet trade is a major pathway of alien animal introductions (Hulme, 2015a). It is estimated that 70 per cent of households in the United States and 38 per cent of households in Europe have pets. In addition to the majority of dogs and cats, fishes, birds, small mammals and reptiles are commonly kept (Mazzamuto *et al.*, 2021). In Europe, a systematic review revealed invasive alien mammal introductions were primarily a result of escapes by pets (69 per cent) and from zoos (50 per cent) and fur farms (38 per cent), while far fewer arose from other agricultural species or biological control and none were reported as contaminants, stowaways or *via* corridors (Tedeschi *et al.*, 2021). Pet escapes and releases are major drivers facilitating vertebrate invasions (e.g., mammals in Brazil (da Rosa *et al.*, 2017) and amphibians and reptiles of the United States (Krysko *et al.*, 2016) and European Union (Hulme *et al.*, 2008; Katsanevakis *et al.*, 2013)).

Pets also have the potential to become important vectors for pathogens and microorganisms that cause disease in animals and humans, in particular pets derived from wild animals (Day, 2011). The spread of monkeypox to humans in the United States is thought to be due to contact with prairie dogs sold as pets (Brown, 2008) and pets are considered to have been important in the transmission of chytridiomycosis and ranaviral disease, which cause severe damage to amphibians (Schloegel *et al.*, 2012).

3.2.3.4 International travel for commerce and tourism

In 2019, there were approximately 1.5 billion international passenger arrivals associated with tourism, a five-fold increase in the number of travellers compared with 1980 (UNWTO, 2021). The continued expansion of the worldwide air transport network has facilitated this global movement of human passengers and, by increasingly linking regions of the world with similar climates, has facilitated the introduction of invasive alien species (Tatem, 2009). While some invasive alien species, particularly mosquitoes (Brown *et al.*, 2012), can be unintentionally transported in commercial passenger aircraft, the highest risk of introducing a wide range of alien species comes from the passengers. Passengers often intentionally transport fresh food items, untreated timber, or animal skin products, either for personal consumption or as gifts, which may carry alien species or alien pathogens as contaminants on the passengers themselves or in their luggage. In the United States, border inspections have found that more than half of all pests encountered were associated with traveller baggage rather than cargo (McCullough *et al.*, 2006). Although some international travellers attempt to intentionally smuggle live animals, plants and food products that could be themselves invasive alien species or harbour them as contaminants (Chown *et al.*, 2012; Soon & Manning, 2018), most international travellers are unaware of the risk they pose in unintentionally introducing stowaways. International travellers can also introduce stowaways on their clothing, footwear and equipment (e.g., tents, fishing tackle and golf clubs). A single gram of soil attached to footwear can harbour 5 million bacteria, 50,000 fungi, 3 seeds and 40 nematodes, and these taxa may often include potential invasive alien species (Hulme, 2015a). When these figures are multiplied up by the more than one billion international travellers worldwide (Glaesser *et al.*, 2017), the global movement of alien stowaways is substantial. Up to half of hikers sampled in mixed evergreen forest in California were found to be carrying *Phytophthora*

Box 3 4 International tourists and scientists visiting Antarctica.

Strong climatic and geographic barriers, attributes associated with low habitat invasibility, naturally isolate Antarctica from the rest of the world (Chwedorzewska *et al.*, 2020). Climate change and an increasing number of visitors (G. A. Duffy *et al.*, 2017; Greve *et al.*, 2017) have weakened these barriers, leading Antarctica to become an area of special concern for the management of biological invasions (**Chapter 6**, **Box 6.10**). An average of 9.5 seeds per visitor are carried to Antarctica every summer (Chown *et al.*, 2012). The highest risk of seed transportation is associated with science programs **(Figure 3.11)** and tourist support personnel rather than with the increasing tourist numbers (Chown *et al.*, 2012; Chwedorzewska *et al.*, 2020; Huiskes *et al.*, 2014). Between the summers of 2019 and 2020, about 74,400 tourists visited Antarctica and 18 nations had established over 50 research stations (Hughes *et al.*, 2020; IAATO, 2020). Alien plants and invertebrate species in Antarctica are found almost exclusively close to visitor sites and research stations (Molina-Montenegro *et al.*, 2012, 2014).

Figure 3 11 **Research stations in Antarctica increase the risk of biological invasions.**

The Australian Antarctic Division has 4 permanent research stations in Antarctica and the subantarctic. Photo credit: David Barringhaus/Australian Antarctic Division – Copyright.

The introduction, establishment and spread of *Poa annua* (annual meadowgrass) in different localities in Antarctica is well documented (Chwedorzewska *et al.*, 2015). *Poa annua*, an annual grass native to Europe and an invasive alien species in the Andes, has been observed in the vicinity of Arctowski Station on King George Island in Antarctica since 1985 (Chwedorzewska, 2008). In this site, *Poa annua* maintains a genetically diverse population, which has been attributed to intense human activity in the station facilitating multiple introductions from different source populations (Chwedorzewska, 2008).

Fuentes-Lillo *et al.* (2017) found a connection between human activity and invasive alien plants in the Fildes Peninsula in King George Island. These authors found higher concentration of seeds in soil samples at sites with increased human activity (i.e., next to dormitories of logistics personnel). Six of the eight alien species recorded in soil samples were also found in King George Island; *Taraxacum officinale* (dandelion) and *Poa annua* have been the most successful colonising alien species in these ecosystems (Fuentes-Lillo *et al.*, 2017).

ramorum, the causal agent of sudden oak death, in soil on their shoes (Davidson *et al.*, 2005). It also appears that tourists visiting caves may be responsible for spreading *Pseudogymnoascus destructans* (white-nose syndrome fungus) in bats (Puechmaille *et al.*, 2011). Similarly, tourists are known to spread weed seeds into national parks (Pickering & Mount, 2010).

The motives and Interests of tourists are also changing with increasing interest in recreational activities (e.g., golf, fishing), agritourism (e.g., winery visits), visits (including camping) to national parks and reserves (Hulme, 2015a). This change in behaviour poses an increased risk of introductions into areas that may not yet been exposed to invasive alien species. The number of passengers embarking on world and extended length cruises is doubling every decade (Klein, 2011) and has permitted access to coastal areas previously exposed to low numbers of visitors. Since 1990, international visitor numbers to the Antarctic continent have increased almost 10-fold (Hulme *et al.*, 2012) and up to half of tourists and visiting scientists unintentionally bring with them seeds of alien plant species which could pose a considerable risk of establishing in the region (Huiskes *et al.*, 2014). Much of this risk is not simply from the tourists themselves but the support crews **(Box 3.4)**. Similar risks are found in the Arctic where people and their luggage are responsible for around 5 per cent of all alien plant introductions (Wasowicz *et al.*, 2020). While the number of international passenger arrivals world-wide has more than doubled since 1990, it is in emerging economies in Africa, Asia and South America where the rate of growth of passenger arrivals has been highest and these regions may be less well prepared to face new risks from invasive alien species (Glaesser *et al.*, 2017). With forecasts of global tourist numbers reaching 1.8 billion international travellers in 2030, combined with new destinations previously less exposed to invasive alien species and more activities in less visited areas, the future risk of introducing invasive alien species appears significant (Hulme, 2015a).

3.2.3.5 Externalities of negative impacts and cost

The introduction of invasive alien species is usually an unintended or intended consequence of economic activities that not only brings species into areas where they were not present, but also affects the frequency of repeated introductions and the spread of established alien species (Touza *et al.*, 2007; **section 3.2.3**). However, control is difficult because those whose actions result in the introduction of invasive alien species are rarely those affected, and they are often not held accountable for their actions (Perrings *et al.*, 2005; Tollington *et al.*, 2017; **section 3.2.1**). For example, in trade of plants and animals, the prices paid by the importer to the exporter include production and transport costs, but usually do not include the costs incurred when animals or plants become invasive. Alien species that lead to improved quality of life and economic benefits are considered public goods, especially in cases where awareness of the impacts of invasive alien species is limited. In addition, the characteristics of public goods, such as “non-rival” and “non-excludable”, create incentives to free-ride and further increase market inefficiency (Marbuah *et al.*, 2014; Touza *et al.*, 2008). These activities of economic agents that affect others without going directly through the market are called “externalitie” (**Glossary**), and externalities that negatively affect other agents are called “negative externalitie” (**Chapter 6**, **section 6.2.1(6)**). The damages and management costs incurred by biological invasions are a typical case of negative externalities arising from economic actions, and for many of the examples listed under **sections 3.2.1**, **3.2.2.3** and **3.2.3.2**, negative externalities are an important explanation for why high rates of invasions are being sustained (**Chapter 2**) despite known negative impacts on nature, nature’s contributions to people and good quality of life (**Chapter 4**).

Internalization of externalities can be a powerful driver to prevent the introduction of invasive alien species (**Chapter 6**, **section 6.2.1.(6)**). But the current situation of leaving externalities unattended without recognizing their existence is a driving force for the introduction of invasive alien species that underlies many social, economic and demographic drivers.

3.2.3.6 Wealth, inequality and poverty

Are invasive alien species primarily a problem of wealthy countries? National GDP has been a frequent metric used to explain variation in the number of alien species among different countries, with countries having a higher GDP being more invaded (Essl *et al.*, 2011; Hulme, 2021b; Seebens *et al.*, 2017). This positive relationship between GDP and the number of alien species in a country appears to hold both across global and regional scales as well as for quite different taxa including fish, mammals, birds, plants and agricultural pathogens (**Chapter 2**, **section 2.1**). Such trends may be indicative that countries with higher levels of consumption tend to facilitate the introduction and establishment of alien species. However, the current number of alien species in a country is the result of a cumulative process where alien species have accumulated over several centuries (**Chapter 2**). Hence, research has shown that historical levels of GDP might be a better predictor of the number of alien species found in a country than the current GDP (Essl *et al.*, 2011). This illustrates that GDP is a flow and that the best measure of a process that, in many countries, has deep historical roots, is the stock of wealth in any country. This wealth measure is the cumulative effect of past investments, and accounts for the assets such as natural capital, produced capital, and human capital that underpin growth and consumption possibilities (Perrings, 2010). Few studies have examined the role of wealth on numbers of invasive alien species, but where it has been examined it has been found to explain a small but significant amount of variation in the numbers of alien species in Europe (Pyšek *et al.*, 2010). Since the wealth of a country is a more important determinant of numbers of alien species than the contemporary GDP, the cumulative build-up of assets which support greater consumption may lead to more immediate increases in numbers of alien species than rapid changes in GDP.

The current combined gross national income of all countries in the world is estimated to be over US$94 trillion, with 10 countries accounting for 68 per cent of this amount (IMF, 2021). The distribution of this wealth is also often highly uneven within countries, so that the 10 per cent richest individuals concentrate 52 per cent of the world income, whereas 50 per cent of the global population accounts for only 8.5 per cent (Chancel *et al.*, 2022). Poverty and marginalization created by economic inequality within and among countries may indirectly drive the introduction, establishment and spread of invasive alien species. For those countries with a lower level of wealth, the warning signs suggest that as the economies grow and build a larger asset base, the risk of alien species introductions might also increase. This risk may be further exacerbated where the route to economic growth and poverty reduction encourages the development of economic sectors based around alien species (**sections 3.2.2.3**, **3.2.3.6**, **3.2.5**, **3.3.1.1**). For example, the invasive alien tree *Prosopis juliflora* (mesquite) was intentionally introduced in many eastern Africa countries to improve the livelihood of communities with very low income subjected to malnutrition and food shortages, as it may be a reliable source of firewood and animal fodder in arid regions (Pasiecznik *et al.*, 2007; **section 3.2.5**, **Box 3.6**); however, the species have become highly dominant in many regions, thus decreasing biodiversity and threatening the water supply (Pasiecznik *et al.*, 2007; **Chapter 4**, **boxes 4.8** and **4.9**). Invasive alien species are also important for the subsistence and income of certain low income communities in South Africa, including the invasive cactus *Opuntia ficus-indica* (prickly pear) in the Eastern Cape Province and multiple alien species cultivated in urban gardens in the Limpopo province (e.g., the invasive tree *Schinus terebinthifolius* (Brazilian pepper tree)). In many cases, it is not clear how the cultivation of these invasive alien species has contributed to their spread (Mdweshu & Maroyi, 2020; Mosina *et al.*, 2015). Some Indigenous Peoples and local communities can also be more inclined to use alien plants if they experience a loss of traditional medicine knowledge and a loss of historically used medicinal plants (IPBES, 2020). In rural Mexico, there are economic incentives to farm the invasive alien fish *Oreochromis* spp. (tilapia) which has been viewed as having a positive impact as a route out of poverty (Martinez-Cordero & Sanchez-Zazueta, 2022). However, there are examples showing that using alien species to promote economic growth may lead to more poverty and inequality, such as the use of *Lates niloticus* (Nile perch), which was introduced into many African lakes (Kelly, 2018; see **section 3.2.5, 3.3.2.1**). In the Lake Victoria basin, the invasion of the Nile perch nearly exterminated native fish populations, and local communities were ultimately forced to shift from traditional fishing, which ensured their subsistence, to catching the invasive alien perch. Nile perch fishing supplies external markets and provides minimum income to households, thus leading to more poverty, malnutrition and lower quality of life (Geheb *et al.*, 2008; **Chapter 4**, **Boxes 4.8** and **4.9**).

3.2.4 Science and technology

While science and technology are major factors underpinning demographic and economic changes, science and technology can also act as indirect drivers of change in nature affecting invasive alien species **(Figure 3.12)**. This section focuses on how research activities (**section 3.2.4.1**), the rise and spread of communication technology (**section 3.2.4.2**), and breeding and genome technologies (**section 3.2.4.3**) can facilitate the transport, introduction, establishment and spread of invasive alien species. Science and technology may interact with economic drivers through the role of information technology in supporting international trade in invasive alien species (**section 3.2.3.1**), and with biological invasions *via* unintended consequences of introducing and/or controlling invasive alien species themselves (**section 3.3.5**). Section 3.2.4 describes evidence for links between specific science and technology drivers and invasive alien species, and makes reference to other indirect and direct drivers when relevant, whereas the specific contribution of science and technology to controlling invasive alien species is dealt with in **Chapter 5**, **section 5.4.4**.

3.2.4.1 Research

Scientific research can involve the transport, rearing, storing, manipulation and experimental release (either under controlled conditions or outdoors) of living organisms. While most evidence to date points to scientific research and related activities as important drivers in the stages of transportation and introduction of invasive alien species, there is a paucity of evidence on their role in establishment and spread.

There are a number of documented examples of use of organisms outside of their native ranges for laboratory research which have resulted in biological invasions. For instance, *Xenopus laevis* (African clawed frog) is the most studied amphibian worldwide and one of the best model organisms for studies in cell, molecular and developmental

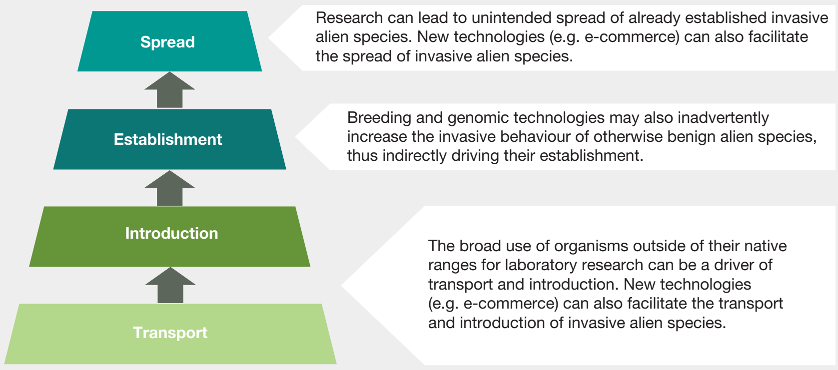


Figure 3 12 **Examples of the role of science and technology in facilitating invasive alien species across stages of the biological invasion process.**

Science and technology can facilitate the transport and spread of invasive alien species *via* their specific use in research and their trade through e-commerce. Breeding and genome technologies may select for traits that increase invasiveness, and research and e-commerce can also facilitate further spread of invasive alien species.

biology. *Xenopus laevis* has been continuously introduced for the past 50 years, and intentionally released in Europe, Asia and North and South America and is likely responsible for the spread of the chytrid fungus of the genus *Batrachochytrium* (Fisher & Garner, 2007, 2020; Weldon *et al.*, 2004). Agronomic research has also led to the introduction of wild relatives of crops outside their ranges. For instance, populations of *Solanum chacoense* (Chaco potato), a wild relative of *Solanum tuberosum* (potato), has established close to research centres where the species was most certainly introduced as part of breeding programs in Australia, China, New Zealand, United States and Argentina (Simon *et al.*, 2010). Unintentional or intentional releases from aquaria have been listed among the major sources of invasive alien invertebrates and fishes in estuaries and rivers (Englund, 2002), and escapes of plant propagules or seeds from botanic gardens is also responsible for some major plant invasions **(Box 3.5)**. In addition, unintentional releases from experimental farms conducting agricultural research (**section 3.3.1.1.4**) are major sources of some of the established populations of highly invasive mammals and birds including *Mustela vison* (American mink), *Myocastor coypus* (coypu), *Ondatra zibethicus* (muskrat), *Nyctereutes procyonoides* (raccoon dog), *Procyon lotor* (raccoon), *Threskiornis aethiopicus* (sacred ibis) and *Oxyura jamaicensis* (ruddy duck) (Barrat *et al.*, 2010).

Devices, sampling gear and equipment used in research activities within natural habitats may act as vectors of invasive alien species. For instance, barnacles frequently attach to the leg-rings used to identify individual wading birds by ornithologists and can be transported long distances along bird migratory routes, "hitch-hiking" with their host birds. Since more than 30 living barnacles can attach to a single ring, this can lead to substantial transportation and introductions to new areas (Tøttrup *et al.*, 2010). More recently, the use of submersible assets, like remote-operated vehicles and human-occupied vehicles, open a novel potential pathway through which scientific research can aid the transport of invasive alien species. In particular, the use of remote-operated vehicles has expanded the reach of human influence to regions where humans themselves cannot access. These high-technology vectors have a tremendous potential to increase transport of invasive alien species in marine ecosystems (Thaler *et al.*, 2015), as illustrated by the transport and potential introduction of living limpets from deep-sea hydrothermal vents to other distant vents (Voight *et al.*, 2012).

3.2.4.2 Development of communication technology

The development of communication technology is an important driving force for the globalization of markets. As of 2021, 63 per cent of the world population (i.e., 4.9 billion people) had internet access, an almost five-times increase compared with 2005, and 95 per cent was covered by broadband mobile network (i.e., 3G and over; International Telecommunication Union, 2021). New distribution channels such as internet trading (e-commerce) have caused significant changes in the movement of organisms. In e-commerce trading surveys, between 30 and 80 per cent of recognized invasive alien plant species were detected on auction sites daily, making it possible to obtain invasive alien plants from almost anywhere in the world (Humair *et al.*, 2015). Due to the difficulty in tracing the contents of express mail, and the increasing volume of trade through this route, the current biosecurity (**Glossary**) system cannot

Box 3 5 **The role of botanic gardens in the introduction of invasive alien plants.**

Botanic gardens **(Figure 3.13)** have made a significant contribution to the collection, cultivation and distribution of plant species for research and scientific uses worldwide (Sharrock, 2011) but have also been implicated in the introduction, early cultivation and/or local spread of invasive alien plant species into global biodiversity hotspots (Hulme, 2011a). Studies exploring the global increase of alien plant species have identified the establishment of botanic gardens as an important driver facilitating biological invasions (Seebens *et al.*, 2017). The global emergence of new alien plant species, defined as the first record of an alien species anywhere in the world, has been found to be related to the number of botanic gardens established in a region (Seebens *et al.*, 2018). A study from China examined the association between the first record of an invasive alien species in a region and multiple possible explanatory factors, including botanic gardens (Ni & Hulme, 2021). The researchers found that botanic gardens, including their history and number of species in living collections, generally play more important roles in influencing the number of first records of invasive alien plants compared to socioeconomic variables (such as Gross Domestic Product) and environmental factors (such as climate). However, invasive alien species primarily introduced for horticultural uses were more influenced by botanic gardens, while those introduced for agricultural uses were more strongly associated with climate variables, and the numbers of species introduced unintentionally were shaped by trade (**sections 3.2.1**, **3.2.3.1** to **3.2.3.4**, **3.3.1.4**). This research is the strongest evidence to date pointing to the role botanic gardens may play in the invasions of ornamental plant species. Despite signing up to the Global Strategy for Plant Conservation, most botanic gardens rarely implement regional codes of conduct to prevent plant invasions, few have a policy for biological invasions, and there is limited monitoring (**Glossary**) of garden escapes (Hulme, 2015b). Given the rapid increase in living collections, especially in Asia, this suggests botanic gardens may become increasingly important for the introduction of alien species in the future.

Figure 3 13 **Botanical gardens facilitate the introduction of invasive alien species.**

The China National Botanical Garden cultivate 6,000 species of plant, including 2,000 kinds of trees and bushes, 1,620 varieties of tropical and subtropical plants, 500 species of flowers and 1,900 kinds of fruit trees several of which are believed to have escaped and become established. Photo credit: Top Photo Corporation, Shutterstock – Copyright.

adequately manage internet trade (Humair *et al.*, 2015). In e-commerce, invasive alien plants are traded over longer distances than traditional commerce in plants, where people visited horticultural nurseries to make their purchases. In particular, seeds of invasive alien plants were transported further than saplings of alien plants (Lenda *et al.*, 2014). In the aquatic alien plant trade, a variety of invasive or import prohibited plants were sold online, and the traders lack knowledge about species identification and regulation. This is also the case for the trade in freshwater aquatic plants for aquaria in Brazil, where unregulated e-commerce has stimulated illegal trade and contributed to the introduction and spread of invasive alien macrophytes (Peres *et al.*, 2018). In the internet trading of ornamental marine life, unregulated e-commerce has contributed to the introduction and spread of invasive alien macroalgae in Europe, North America and Australia (Walters *et al.*, 2006). Many wholesalers and retailers lack awareness of the potential risks of ornamental marine species (Morrisey *et al.*, 2011). Online trading of freshwater invasive alien crayfish as pets is prevalent and has become a major route of biological invasions of crayfish and their contaminants and stowaways in many parts of the world (Chucholl, 2013; Faulkes, 2010, 2015; Papavlasopoulou *et al.*, 2014). E-commerce and social media also have supported an extensive world trade network of alien ornamental freshwater fishes, where customers often also have little knowledge of the risks of releasing these invasive alien species in the wild (Magalhães & Jacobi, 2010; Mazza *et al.*, 2015).

3.2.4.3 Breeding and genomic technologies

The modification of phenotypic traits to increase biomass, growth, and resistance to pests, diseases and stressors, etc., can increase the invasion potential of species that otherwise would not be invasive (e.g., Flory *et al.*, 2012 and references therein). Plant and animal traits that have traditionally been modified through breeding, selection and hybridization can now be more effectively modified *via* genomic technologies. The application of these techniques to crop and stock species has catalysed debates over the invasive potential of these "novel taxa" and how to adapt invasive alien species risks assessments and biosafety measures to deal with them (Hoenicka & Fladung, 2006; Luke Flory *et al.*, 2012; Quinn *et al.*, 2015; **Chapter 5**, **section 5.4.4.2**).

Studies suggest that risks posed by novel taxa are often inevitable and can vary spatially, temporally and according to the type of organism and the purpose of the trait selection process (Ellstrand *et al.*, 2013). There is good evidence that traditional breeding of plant species native to other regions for ornamental purposes has increased their invasive potential in North America (Ross *et al.*, 2008; Wilson & Mecca, 2003). For example, cultivars of the ornamental Asian shrub *Ardisia crenata* (coral berry) artificially selected for dense foliage show higher competitive ability and seedling recruitment success than native populations, which likely favours their dominance in the understory of mesic forests in Florida (Kitajima *et al.*, 2006). The ornamental clonal herb *Kalanchoe × houghtonii* (Houghton's hybrid), which is an artificial hybrid obtained from the crossing of two species endemic to Madagascar (*Kalanchoe daigremontiana* (devil's backbone) and *Kalanchoe delagoensis* (chandelier plant)) that exhibits a highly effective clonal growth which possibly has contributed to its wide distribution and local dominance in tropical arid and semi-arid ecosystems (Guerra-García *et al.*, 2015; Herrando-Moraira *et al.*, 2020). There is concern that the invasive potential of some pasture grasses has increased as a result of intensive artificial selection, which has used multiple tools (e.g., ploidy manipulation and introduction of endophytes) to maximize grass productivity under the specific conditions of each region of interest (Driscoll *et al.*, 2014). Transgenes for herbicide resistance present in the genetically modified *Agrostis stolonifera* (creeping bentgrass) used as lawn grass were found in wild *Agrostis* populations, suggesting that the resulting novel genotypes may be persistent and possibly favour these genetically modified organisms outside cultivation (Reichman *et al.*, 2006). Similar or even higher risks may apply to the selection of bioenergy crops (Richardson & Blanchard, 2011); for example, selection for fertility in the highly productive *Miscanthus × longiberbis* (giant miscanthus cultivar) led to a high increase in its potential to escape cultivation (Smith *et al.*, 2015). Among invasive alien trees, selection for high timber and forage production may have indirectly increased the invasion potential of a cultivar of the tropical tree *Leucaena leucocephala* subsp. *glabrata* (white leadtree) in certain areas in Northeast Australia (C. S. Walton, 2003). Similarly, provenance forestry trials and common garden experiments designed to select the seed sources of alien pine species most likely to succeed under distinct conditions in the introduced range possibly contributed to the high invasion success of some of these species in South America (Zenni, 2014; Zenni *et al.*, 2017).

There is evidence that human selection of specific behaviours in the hybrid fish *Xiphophorus hellerii × maculatus* (red swordtail) contributed to the emergence of established invasive alien populations in Hawaii, with a behaviour syndrome characterized by high aggression and exploration (D'Amore *et al.*, 2019). Among invertebrates, the artificial hybrid between European and East African honeybee species shows superior pollen extraction ability and higher swarming rate (i.e., the process of colony splitting to generate new colonies) than the European species (Pesante *et al.*, 1987), which may have contributed to its spread in the Americas to the detriment of native pollinators (Santos *et al.*, 2012).

Cultivating genetically modified crops may also indirectly favour the spread of invasive alien pests and pathogens; for example, the invasive tomato moth, *Tuta absoluta* (tomato leafminer), has been found to establish and spread rapidly in farms planted with genetically modified tomato cultivars, whereas traditionally bred cultivars have been shown to be resistant to this pest (Rakha *et al.*, 2017). As an example of how artificial selection may indirectly favour vertebrate invasions, intensive artificial selection has increased the fecundity of domestic pigs, so that hybridization and admixture between populations of domesticated pigs and wild boar have been associated with feral swine genotypes with higher fitness and hence more likely to establish and spread in natural ecosystems beyond the species' range in Europe (Canu *et al.*, 2018; Fulgione *et al.*, 2016; Goedbloed *et al.*, 2013), North America (Smyser *et al.*, 2020) and South America (de Oliveira *et al.*, 2018).

3.2.5 Policies, governance and institutions

Policies, governance and institutions underlie most direct and other indirect drivers of change in nature in complex ways. For example, economic drivers (**section 3.2.3**) are strongly linked to policy and institutional drivers, which govern production through regulations, taxes and subsidies, and affect terrestrial, aquatic and marine bioproduction systems, which in turn facilitate biological invasions (**section 3.3.1**). A common thread running through many of these systems is that policies, governance and institutions are focussed on the economic and production systems, with consequences for biological invasions receiving little attention. These unintended consequences are the focus of this section, which deals with regulations, taxes and subsidies that may result in unintended facilitation of the introduction, establishment and spread of invasive alien species (**Figure 3.14)**. The role of policies and institutions explicitly tasked with the control of invasive alien species and management of biological invasions are addressed in **Chapter 6**.

In an era of globalization and increasing interconnectedness between people, states and regions, there is an increasing reliance on supranational arrangements for the organization of human societies, referred to as international institutions and organizations. The annual amount of international official assistance for development has increased from less than US$80 billion in 2000 to over US$127 billion in 2010, particularly as a result of increasing bilateral disbursements to low-income countries (World Bank & International Monetary Fund, 2012). By providing the regulatory frameworks for transboundary activities, international institutions and organizations may act as indirect drivers facilitating the uptake, transportation, establishment and spread of invasive alien species, due to promotion of other indirect demographic and economic drivers of change in nature such as migration (**section 3.2.2.2**), trade (**section 3.2.3.1** to **3.2.3.3**) and human travel (**section 3.2.3.4**). In addition, international institutions and organizations may also influence direct drivers of change in nature, including the deployment of infrastructure (**section 3.3.1.4**), introductions from agriculture, forestry, fisheries and aquaculture (**sections 3.2.3.2**; **3.2.3.3** and **3.3.1.1**), and multilateral measures against climate change which may again facilitate invasive alien species. Moreover, international agreements and supranational decisions may scale down to national governance, an indirect driver of change which may facilitate invasive alien species (**section 3.2.5**). Although the role of governance in facilitating invasive alien species has been occasionally evaluated (Evans *et al.*, 2018), with a few exceptions (Mwangi & Swallow, 2008; Pérez *et al.*, 2003), there is a paucity of studies specifically addressing the role of international organizations and institutions in managing biological invasions. While it is hard to draw overall geographical patterns because of the global scale of this driver, its influence is expected to be global. This section illustrates the issue of international institutions and organizations acting as an indirect driver promoting invasive alien species by facilitating different stages of the biological invasion process.

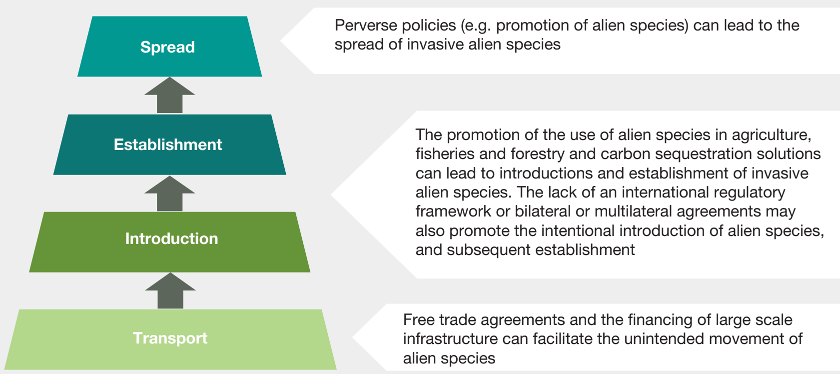


Figure 3 14 **Examples of the role of policies, governance and institutions in facilitating invasive alien species across stages of the invasion process.**

Free trade agreements, finance, promotion of species for use in agriculture, fisheries or forestry outside their native range, lack of regulatory frameworks and unintended consequences (active promotion of invasive alien species for other benefits, without consideration of risks) are some examples of drivers of changes in nature facilitating invasive alien species across invasion stages.

International funding agencies for economic development and regional integration may indirectly influence the uptake, and transport of invasive alien species by financing large scale infrastructure that facilitates the unintended movement of alien species (e.g., navigation channels and tunnels; Hulme, 2015b). In addition, international funding agencies may facilitate the introduction, release, and establishment of invasive alien species by actively promoting the use of alien species in agriculture, fisheries and forestry and carbon sequestration solutions (**sections 3.2.3.2**; **3.3.1.1**). An emblematic example is the promotion of the highly invasive leguminous tree *Prosopis juliflora* (mesquite; **section 3.2.3.6**; **Box 3.6**) from Central and South America into many arid and semi-arid regions of the world. Similarly, *Pontederia crassipes* (water hyacinth) has been promoted by international aid agencies in Africa for biomass production (**section 3.5.2**, **Box 3.12**). Its spread rapidly affected water flow regimes, impeding hydroelectric power production, water quality and fisheries (Batanouny & El-Fiky, 1984). In Vanuatu, the Central American woody species *Cordia alliodora* (Ecuador laurel) introduced to promote timber production, invaded native ecosystems and ultimately turned out to be unsuitable for timber production in that climate (Tolfts, 1997). Alien plants were introduced in many countries for economic development, including Tonga (Space & Flynn, 2001). *Lates niloticus* (Nile perch; **Chapter 4**, **Box 4.10**) is a notable example of an invasive alien species arising from aid-related fish introductions. This species was first introduced into Lake Victoria, East Africa, in the mid-1950s to supplement dwindling fish stocks. The population took 20 years to build up, but the Nile perch has since had a substantial impact on the ecological balance of the lake (Ogutu-Ohwayo, 1998), and is implicated in the extinction of more than 200 endemic fish species (Lowe *et al.*, 2000). Lake Victoria has been described as a major evolutionary and ecological disaster caused by the release of an invasive alien species, although the relative contributions and cause-effect relations between invasive alien species and other concurrent drivers of change in nature have been hotly debated (Marshall, 2018; van Zwieten *et al.*, 2015; **Chapter 4**, **Box 4.10**). More generally, international aid and assistance programmes have actively promoted the use of farmed plants, fish and animals in new regions, many of which are invasive and/or are hosts of other invasive alien species (**sections 3.2.2.3**; **3.3.1.1**).

Free trade agreements, being treaties between two or more countries or states to facilitate trade and eliminate trade barriers, increase the flux of goods between regions and may facilitate the uptake and transportation of invasive alien species, either as subject of commerce (when traded goods are living organisms), or more frequently as by-product of transport (e.g., unintentional introductions in ballast water, as stowaways in packaging and cargo, or as contamination of crop products with agricultural pests). Furthermore, the World Trade Organisation (WTO) in an attempt to prevent quarantine laws becoming trade barriers has discouraged nations from using quarantine laws to stop the spread of invasive alien species (Riley, 2005), illustrating the challenge of addressing national policies that drive biological invasions to account for the transboundary aspect of biological invasions (Hulme, 2015a).

More recently, as economic multilateral instruments have been developed to tackle climate change, taxes based on carbon and carbon-trading markets (e.g., Reducing Emissions from Deforestation and forest Degradation (REDD+)) have been implemented under the international governance framework of the Kyoto Protocol (United Nations, 1997). Such initiatives are a possible driver for the establishment and spread of invasive alien species, such as fast-growing trees from large-scale plantations for carbon

Box 3 6 National and international policies resulting in the introduction and spread of *Prosopis juliflora* (mesquite), as reported by Indigenous Peoples and local communities.

In Botswana, Ethiopia, India, Jordan and Kenya, Indigenous Peoples and local communities have reported the intentional introduction of *Prosopis juliflora* (mesquite) by governments and associated international programs with the aim of halting land degradation, controlling desertification and deforestation and improving the good quality of life of the local communities (Al-Assaf *et al.*, 2020; Becker *et al.*, 2016; Haregeweyn *et al.*, 2013; Linders *et al.*, 2020). In Kenya for instance, the Chamus pastoralists report that *Prosopis juliflora* was introduced twice: first in 1973 through a government initiative; and 10 years later, through the Fuelwood Afforestation Extension Project, a joint initiative from the Food and Agricultural Organization (FAO) and the Government of Kenya (Becker *et al.*, 2016). In Ethiopia, the Afar recall that the species was introduced in the 1980s in state farms and settlements to improve the microclimate, provide shade, halt land degradation, provide fuel wood, as a source of pods for fodder, and to increase sustainability of livelihoods in the Afar region of Ethiopia (Linders *et al.*, 2020). In India, Indigenous Peoples and local communities report that *Prosopis juliflora* was introduced to ameliorate saline soils, and as a source of timber, fuelwood and fibre in the latter half of nineteenth century; and that the species was later promoted by the government from the 1970s onward to combat desertification and soil salinization in North-West India (Duenn *et al.*, 2017).

sequestration (Dickie *et al.*, 2014; Lindenmayer *et al.*, 2012). In fact, a global survey of 226 carbon projects shows that 6 per cent use predominantly alien species and 18 per cent use a mixture of native and alien species (Lindenmayer *et al.*, 2012). Dickie *et al.* (2014) list *Acacia*, *Casuarina* (beefwood), *Eucalyptus, Falcataria* (peacocksplume), *Pinus* (pine) and *Pseudotsuga* (douglas-fir) as major invasive alien genera commonly used for carbon sequestration (**section 3.3.1.1.2**). Similarly, recommendations to introduce alien tree species into British native woodlands as part of adaptive management (**Glossary**) strategies to mitigate rapid climate change, and the potential impacts of associated pests and diseases, will increase the risk of biological invasions as well (Ennos *et al.*, 2019). Overall, although the role of international organizations as indirect drivers facilitating biological invasions has largely been neglected, the evidence to date suggest they may play a role in transport and introduction (*via* trade and infrastructure, see **section 3.2.3.1**) and release and establishment (*via* agriculture, forestry and aquaculture, see **section 3.3.1.1**), which deserves further attention.

Furthermore, international and national programs targeted at biological control of existing pests have resulted in the widespread introduction of invasive alien species. Since 1955, *Euglandina rosea* (rosy predator snail) has been introduced to at least 27 island groups and continental countries, including many Pacific islands, in most cases with the aim of controlling the invasive *Lissachatina fulica* (giant African land snail). The effects in terms of control of the African snail have been limited, but these releases have been catastrophic to many native species; *Euglandina rosea* has caused the extinction of 134 land snail species and the declines of many more species (Gerlach *et al.*, 2021). The introduction of *Gambusia affinis* (western mosquitofish) and *Gambusia holbrooki* (eastern mosquitofish) in most temperate and tropical countries as biological control agents for mosquitoes started in the early 1990s and continues to date. These species are now the most widespread fish in the world, recorded in six continents. Mosquito fish have strong negative effects on freshwater ecosystems and on native fish through predation on juveniles and eggs and/or through competition with species with similar ecological niches (W. E. Walton *et al.*, 2012).

Indigenous Peoples and local communities have also reported that national policies limiting land tenure and access rights can be significant drivers of invasive alien species on their lands (IPBES, 2022b). Indigenous Peoples and local communities will often monitor and manage the numbers of invasive alien species and their impacts on their lands and waters (**Chapter 5**), but their ability to do this is greatly reduced if they do not have access or clear ownership of the lands and waters. Access is indeed crucial for monitoring and management, and land tenure can be essential for communities to actively manage their environments. Moreover, many Indigenous Peoples and local communities actively defend their lands from encroachment by industry and other disruptive influences that can also be drivers for invasive alien species (e.g., deforestation; **section 3.3.1**). Lack of clear land tenure or access rights can also prevent Indigenous Peoples and local communities from effectively defending their lands against this environmental degradation, which can in turn lead to an increase in invasive alien species. Indigenous Peoples and local communities have also noted that lack of access to lands and waters and lack of land tenure can lead to communities leaving.

3.3 THE ROLE OF DIRECT DRIVERS OF CHANGE IN NATURE, NATURAL DRIVERS AND BIODIVERSITY LOSS ON INVASIVE ALIEN SPECIES

This section examines five classes of direct drivers of change in nature that together encompass major human influences on the distribution and abundance of invasive alien species **(Table 3.1)**. The definition and classes of drivers are sourced from the IPBES Global Assessment (IPBES, 2019) but adapted for the purposes of invasive alien species by selecting drivers of relevance for biological invasions. This section thus considers land- and sea-use changes, including farming, fishing, logging (**section 3.3.1**); direct exploitation of natural resources, such as mining and species harvesting (**section 3.3.2**); pollution, including both aerial, soluble and solid waste, with a focus on eutrophication and marine debris (**section 3.3.3**); climate change, including both long-term trends and climatic variability, as well as CO_2 fertilization, changes in climate-related extremes and sea level rise (**section 3.3.4**), and the role of invasive alien species and the management of biological invasions, through biotic facilitation and biological control (**section 3.3.5**). Each subsection first assesses the overall trends in and influence of the driver on invasive alien species, including interlinkages with other drivers, and then, where data allow, notes the specific effects of the drivers on particular biomes, taxonomic groups and units of analysis.

3.3.1 Land- and sea-use change

Land-use change is the major driver of change in nature causing loss of biodiversity and natural habitats globally, affecting close to 75 per cent of ice-free land areas (IPBES, 2019). Agriculture and forestry are major causes of land-use change, for example, global crop production has increased by about 300 per cent since 1970, with crops now occupying half of the habitable land on Earth (IPBES, 2019). Much of the information available for sea-use change is within the context of climate change and specifically changes in physical and biogeochemical properties of the ocean in response to climate warming (IPCC, 2019). However, degradation and loss of natural habitats can occur with many sea-uses, including mining and mineral extraction, coastal developments, land reclamation, wind energy and recreational aquaculture (Vrees, 2021). Some of these sea-uses are anticipated to remain at a constant level but increases are forecast for others. For example in the North Sea, surface mineral extraction, water sport recreation, wind farms and possibly mariculture are all projected to increase (Vrees, 2021). Land- and sea-use change stem from major economic (**section 3.2.3**) and demographic (**section 3.2.2**) indirect drivers.

According to some Indigenous Peoples and local communities, land- and sea-use change is the main driver affecting the establishment and spread of invasive alien species on their lands and seas (**section 3.6.2**, **Box 6.13**). A recent review of native and invasive alien plant, vertebrate and invertebrate biodiversity on islands revealed that number and abundance of alien species are generally higher in areas affected by land-use (plantation forests, agricultural or urban sites) as compared to native habitat (794 alien taxa assessed), whereas the opposite is the case for native biodiversity (5517 native taxa assessed; Sánchez-Ortiz *et al.*, 2020). Habitat fragmentation and agricultural intensification were found to be the most commonly studied drivers facilitating plant invasions in a review by Vilà & Ibáñez (2011), with few studies focusing on the roles of habitat loss, land abandonment and afforestation. Land-use changes, in particular agricultural practices, are an important driver facilitating the spread of fungal and bacterial plant pathogens (Anderson *et al.*, 2004). Studies on alien pathogens tend to highlight their role within agricultural, horticultural or forestry systems, however, with less focus on spread to native systems (Anderson *et al.*, 2004; Panzavolta *et al.*, 2021).

Land- and sea-use change can affect invasive alien species in two main ways, firstly, by directly increasing the rate of introduction of alien species (**section 3.3.1.1**), either intentionally (e.g., through the specific use of alien crops and livestock), or unintentionally (e.g., as contaminants of agricultural or aquacultural commodities). Secondly, a variety of land- and sea-use change related processes increase the vulnerability of native ecosystems to invasive alien species (Vilà & Ibáñez, 2011), including habitat fragmentation (**section 3.3.1.2**), establishment of corridors of disturbed habitat through which alien species can spread (**section 3.3.1.3**), deployment of infrastructure (**section 3.3.1.4**), altering disturbance regimes (**section 3.3.1.5**), or other forms of anthropogenic landscape degradation (**section 3.3.1.6**). **Section 3.3.1** thus describes evidence for links between specific land- and sea-use change drivers and invasive alien species (**Figure 3.15)**, and makes reference made to other indirect and direct drivers when relevant. The demographic and economic indirect drivers behind these land- and sea-use change are described in **section 3.2**.

3.3.1.1 Intentional or unintentional introductions from the use of alien species in terrestrial and marine bioproduction systems

Industries based around the growth and harvest of biological resources, including agriculture, aquaculture, forestry, biofuel and carbon sequestration, forage production and

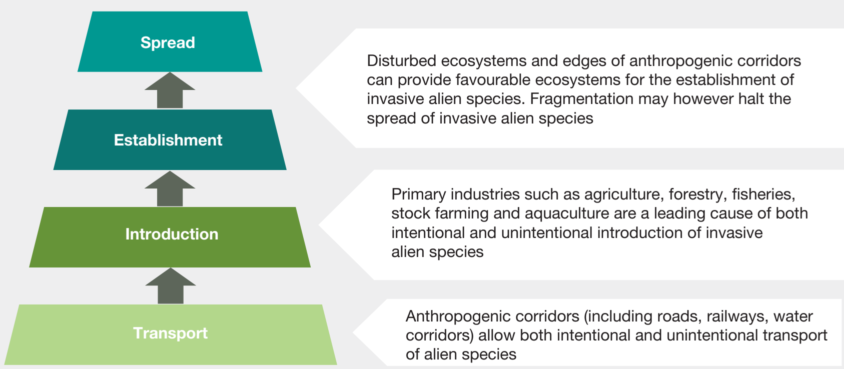


Figure 3 15 **Examples of the role of land- and sea-use change in facilitating invasive alien species across stages of the biological invasion process.**

Anthropogenic corridors can facilitate both the intentional and unintentional transport of invasive alien species, primary industries can facilitate their introduction, and disturbance can facilitate their establishment and spread.

agriculture, are an important cause of the introduction of invasive alien species, both intentionally (e.g., release of plants, animals, or organisms used for pest or weed control into terrestrial or aquatic environments) and unintentionally (e.g., spread of weeds, pathogens, pests and escape from fields/plantations or other containment) (Hulme *et al.*, 2008). Invasive alien species, particularly those from agricultural systems, can facilitate the spread and establishment of pathogens that would otherwise be absent from the introduced range and may pose risks for disease transmission for humans, domestic animals and other native wildlife (Chinchio *et al.*, 2020).

3.3.1.1.1 Aquaculture

Aquaculture (farming of marine organisms) is the largest sector worldwide, after shipping, responsible for introduction of marine alien species (Ojaveer *et al.*, 2018; Bailey *et al.*, 2020). Although the production of marine fish and crustaceans has grown since the millennium, it is now eclipsed by the live-weight volume of marine bivalves and seaweeds which has grown, respectively, from 10 and 11 to 18 and 32 million tonnes per annum between 2000 and 2018 (FAO, 2021). Both the farmed species and/or storage (and other) infrastructures (e.g., cages, nets, floats and ropes) serve as agents of intentional and unintentional introductions and spread of invasive alien species (Campbell *et al.*, 2017). Farmed species are either placed in the sea in enclosures (cages, net pens, rafts), or intentionally released into the environment (Naylor *et al.*, 2001). Intentional introductions comprise both legal and clandestine translocations (Özcan & Galil, 2006; Stentiford & Lightner, 2011; Megahed, 2014). Unintentional introductions consist of "spillover" from crops farmed or stocked in natural habitats (e.g., marine algae farming, marine stock enhancement); escape, unintentional release, or spawning from culture facilities (Arechavala-Lopez *et al.*, 2018, 2017); and alien species associated with the farmed species, or equipment used for culture or transportation of the farmed species (Reise *et al.*, 1998; Mineur *et al.*, 2007). Arguably, due to the high permeability of marine farming facilities, the use of alien species in these settings are essentially intentional introductions to the wild (FAO, 1995; Grosholz *et al.*, 2015). *Tilapia* species are the third most important fish in aquaculture globally, and have established as alien in every country where they have been introduced (Canonico *et al.*, 2005). *Magallana gigas* (Pacific oyster) is one of the most widely used marine invertebrates, introduced primarily for aquaculture in 66 countries, of which alien populations have established in at least 17 (Herbert *et al.*, 2016). The open sea farming of *Undaria pinnatifida* (Asian kelp) and carrageenan-producing seaweeds *Kappaphycus alvarezii* (elkhorn sea moss) and *Eucheuma denticulatum* (eucheuma seaweed), has facilitated their spread to surrounding areas, including marine protected areas, in European, Indian, South America and African coastal waters (Floc'h *et al.*, 1991; Chandrasekaran *et al.*, 2008; Barrios *et al.*, 2007; Tano *et al.*, 2015).

Freshwater aquaculture involves mainly fish (De Silva *et al.*, 2009; Teletchea, 2019) and crayfish (Lodge *et al.*, 2012; Madzivanzira *et al.*, 2021). Globally, the number of alien freshwater fish species is positively correlated with aquaculture production (Gozlan, 2008), and the establishment of alien species from aquaculture has been documented for all continents where introductions have occurred (Britton & Orsi, 2012; De Silva *et al.*, 2006; De Silva, 2012; Gozlan, 2008; Lin *et al.*, 2015; J. Liu & Li, 2010; Luo *et al.*, 2019; Nunes *et al.*, 2015; Ortega *et al.*, 2015; Saba *et al.*, 2020; Shelton & Rothbard, 2006; Q. Wang *et al.*, 2015). Aquaculture is a major source of invasive alien species at national and regional scales. Of the approximately 500 documented introductions of freshwater fishes in the Mediterranean basin, more than 35 per cent are associated with aquaculture (Tricarico, 2012). In the Balkans, 36 species of freshwater fish have been introduced into inland waters *via* aquaculture (Piria *et al.*, 2018). In California, 126 alien species associated with commercial aquaculture have been reported, of which 106 have become established and are negatively affecting native species.

Parasites of a wide range of farmed marine organisms also appear as invasive alien species worldwide. *Haplosporidium nelsoni* (MSX oyster pathogen), a parasite of the Pacific oyster, has spread to estuaries from Maine to Florida, affecting the native *Crassostrea virginica* (eastern oyster; Andrews, 1984; Burreson *et al.*, 2000). Outbreaks of the intrahemocytic parasite *Bonamia ostreae*, protozoan parasite *Marteilia refringens*, two species of parasitic copepods *Mytilicola orientalis* (oyster redworm) and *Myicola ostreae* and the ostreid herpesvirus (OsHV-1), affect farmed Pacific oysters and all originate from imports of stock (Mineur *et al.*, 2014). *Anguillicola crassus*, a blood feeding swimbladder parasitic nematode in eels native to eastern Asia, was widely introduced with its host, *Anguilla japonica* (Japanese eel), to Europe and North America, where it is now widespread in native eel populations sometimes at a prevalence up to 82 per cent of adult and juvenile eels (Barse *et al.*, 2001; Aieta & Oliveira, 2009; T. C. Pratt *et al.*, 2019; Warshafsky *et al.*, 2019). The illegal importation of penaeid prawns from Turkey into Italy was revealed only when the white spot disease was detected (Stentiford & Lightner, 2011). The high concentration of salmon farming in seas off Europe and Canada has been implicated in outbreaks of sea lice (*Lepeophtheirus salmonis* (salmon louse), *Caligus* spp.) in wild salmon (*Oncorhynchus gorbuscha* (pink salmon), *Oncorhynchus keta* (chum salmon)) in these waters (Krkošek *et al.*, 2005). Farmed pacific oysters have served as primary and secondary vectors for the introduction for algae, invertebrates and pathogens affecting both farmed and native oysters (Wolff & Reise, 2002; Mineur *et al.*, 2007, 2014; Verlaque *et al.*, 2015), including invasive alien species such as *Gracilaria vermiculophylla* (black wart weed), *Codium fragile* (dead man's fingers), *Sargassum muticum* (wire weed), *Undaria pinnatifida* (Asian kelp), the sea squirts *Botrylloides violaceus* (violet tunicate), *Didemnum vexillum* (carpet sea squirt) and *Styela clava* (Asian tunicate).

Fish breeds such as farmed *Salmo salar* (Atlantic salmon) have undergone domestication, i.e., intensive selective breeding, and a limited pool of domesticated broodstock, eggs and sperm is shared worldwide (Roberge *et al.*, 2008; Solberg *et al.*, 2020). In the past half century tens of millions of farmed salmon have escaped into the wild (Wringe *et al.*, 2018). Interbreeding between farmed and wild Atlantic salmon in Norwegian waters has altered age and size at maturation in 62 wild salmon populations, caused widespread changes to fitness-related life-history traits, thus threatening already vulnerable wild populations (Karlsson *et al.*, 2016; Bolstad *et al.*, 2017). Interbreeding between farmed and wild conspecific populations is also found in *Sparus aurata* (gilthead sea bream), *Dicentrarchus labrax* (European sea bass), *Argyrosomus regius* (brown meagre) and *Gadus morhua* (Atlantic cod) (Somarakis *et al.*, 2013; Jørstad *et al.*, 2014; Izquierdo-Gómez *et al.*, 2017; Arechavala-Lopez *et al.*, 2017, 2018). *Symphodus melops* (corkwing wrasse), used to control sea lice in salmon farms, also escapes and hybridizes with individuals in local populations (Faust *et al.*, 2018).

3.3.1.1.2 Forestry, agroforestry, biofuel and carbon sequestration

Trees and shrubs have been introduced globally for wood production, fruit and seed crops, erosion control, live fences and building material (Richardson, 1998; Richardson & Rejmánek, 2011; van Kleunen *et al.*, 2020). Of introductions of invasive alien trees and shrubs, 13 per cent were attributed to forestry, 10 per cent to food, and seven per cent to agroforestry (Richardson & Rejmánek, 2011). Many trees extensively used in forestry have high potential to become invasive alien species, including the genera *Pinus* (Richardson, 2006; Fernandes *et al.*, 2016; Brundu *et al.*, 2020), *Acacia* (Donaldson *et al.*, 2014; Richardson *et al.*, 2011, 2015) and *Eucalyptus* (Bennett, 2010; Forsyth *et al.*, 2004; Hirsch *et al.*, 2020; Simberloff & Rejmanek, 2011). Of the roughly 100 *Pinus* species, at least 17 species are now considered as invasive alien species in natural ecosystems, particularly in the southern hemisphere (Richardson & Blanchard, 2011; Richardson & Nsikani, 2021). Of the approximately 200 *Eucalyptus* species cultivated within South Africa (Henderson, 2009), six are listed as invasive alien species by the National Environmental Management Biodiversity Act. Studies in the Iberian Peninsula also show *Eucalyptus globulus* (Tasmanian blue gum) can spread from plantations (Fernandes *et al.*, 2016). *Acacia* species from Australia are widely distributed invasive alien species (Le Maitre *et al.*, 2011). Over 70 *Acacia* species were introduced throughout South Africa for forestry, dune stabilization and ornamental use during the 19th and 20th centuries (Bennett, 2011). Of these 70 introduced species, 14 are now considered to be invasive alien species, four of which arose from commercial forestry plantations (Van Wilgen *et al.*, 2011). The southern hemisphere (e.g., South America, Oceania) has been particularly affected by tree invasions, because of the massive scale of commercial plantations and the absence of competition by native tree species (García *et al.*, 2018; Nuñez *et al.*, 2017; Richardson *et al.*, 2021).

Increased interest in biomass-based energy has increased the use of alien species with rapid growth rates, ease of establishment, wide environmental tolerances, and prolific seed production in plantations, characteristics that also promote them as potential invasive alien species (Barney & DiTomaso, 2008; Leakey, 2009; Richardson & Blanchard, 2011). Across the south-eastern United States, *Eucalyptus* species are commonly utilized for bio-energy (Callaham *et al.*, 2013; Lorentz & Minogue, 2015), and have the potential to invade surroundings woodlands (Callaham *et al.*, 2013). Large stature grasses, such as bamboo, are also used as common biofuel crops, with "running" bamboo species noted to present a significantly higher risk of biological invasion than "clumping" species (Lieurance *et al.*, 2018). The perennial grasses *Miscanthus sinensis* (eulalia) and *Miscanthus sacchariflorus* (Amur silvergrass), planted for ornamental and biofuel uses, also pose high risks across Europe and North America, especially in grassland and tall herb vegetation, ruderal habitats and roadsides (Schnitzler & Essl, 2015). Climate modelling indicates *Miscanthus* (silvergrass) species have already been introduced to most of the suitable regions in the northern hemisphere, whereas there is climatic potential for further expansion in the southern hemisphere, suggesting increased future biological invasion threat there (Hager *et al.*, 2014).

Food forestry, whereby a diversity of food plants is planted in natural or seminatural forested ecosystems, may represent an emerging pathway for the introduction, establishment and spread of alien species into natural or near-natural ecosystems. For example, a recent study identified almost 500 alien species used in the fast-growing food forestry sector in the Netherlands alone, including a number of high -risk invasive aliens including *Akebia quinata* (five-leaf akebia), *Helianthus tuberosus* (Jerusalem artichoke), *Rhus typhina* (staghorn sumac), *Rosa rugosa* (rugosa rose) and *Vaccinium macrocarpon* (cranberry) (Hoppenreijs *et al.*, 2019).

Plantation forests are also hotspots (invasion hotspot in the **Glossary**) for unintentional introductions of invasive alien species In a global review of invasive alien plants, vertebrates and invertebrates on islands (794 alien species), plantation forests had consistently higher numbers and abundances of alien species as compared to native habitat (Sánchez-Ortiz *et al.*, 2020). Invasive forest pathogens have been responsible for many disease outbreaks across commercial, natural and urban forest ecosystems, and generally occur as a result of unintentional introductions *via* containment or stowaway (Burgess *et al.*, 2016; Migliorini *et al.*, 2015; Paap *et al.*, 2020). Notable examples include; *Cryphonectria parasitica* (blight of chestnut), *Ophiostoma novo-ulmi* (Dutch elm disease), *Phytophthora cinnamomi* (Phytophthora dieback), *Phytophthora ramorum* (sudden oak death) and *Hymenoscyphus fraxineus* (ash dieback) (Brasier & Buck, 2001; Pautasso *et al.*, 2013; Rigling & Prospero, 2018; Rizzo & Garbelotto, 2003; Shearer *et al.*, 2007).

3.3.1.1.3 Forage production and livestock grazing

Forage production and pastures for domestic herbivores is a major land-use in almost all biomes of the world (Brondizio *et al.*, 2019). Management of such lands is a major source of biological introductions, because species sown or planted for forage, or weeds associated with these land-uses, may escape and spread into natural ecosystems (Nuñez *et al.*, 2017; O'Connor & van Wilgen, 2020; Pándi *et al.*, 2014). In a survey by Driscoll *et al.* (2014), 91 per cent of grasses developed by agribusiness for pasture were listed as weeds somewhere in the world, and often in the same countries where they were actively been developed and marketed. Policies aiming to facilitate pastoral development can also be responsible for introductions, such as occurred for the pasture grass *Andropogon gayanus* (tambuki grass) in Australia (Cook & Dias, 2006), which is now known to increase wildfire intensity, and transform species-rich savannah systems into alien-dominated grasslands (Driscoll *et al.*, 2014; **section 3.2.5**). In Texas, United States, alien grass species were seen as the future of forage production during the early twentieth century, and several introduced species have since escaped pasture cultivation: *Bothriochloa ischaemum* (yellow bluestem), *Dichanthium annulatum* (Kleberg's bluestem), *Dichanthium aristatum* (angelton bluestem), *Cenchrus ciliaris* (buffel grass), *Megathyrsus maximus* (Guinea grass), *Eragrostis lehmanniana* (Lehmann lovegrass) and *Cynodon dactylon* (Bermuda grass) (Wied *et al.*, 2020). Several of these economically important pasture grasses are invasive alien species throughout several countries. *Megathyrsus maximus*, with its high yield, palatability and tolerance of herbivory is now considered a weed species throughout Africa, America, Australia and Asia (Randall, 2017; Rhodes *et al.*, 2021). *Cenchrus ciliaris* has become a problematic species across Australia, the United States, Mexico and South America (V. M. Marshall *et al.*, 2012) and Bermuda grass now also has a cosmopolitan distribution and is considered one of the world's worst weeds (Randall, 2017; Way, 2014). Some invasive alien species in agricultural systems were introduced through planting of windbreaks and hedgerows, including the globally versatile *Ulex europaeus* (gorse), one of the most invasive alien species in the world, introduced from Europe to Australia, Chile, New Zealand, Sri Lanka and the United States (Roberts & Florentine, 2021). In Southern Africa, invasive alien *Opuntia* (pricklypear) species were initially grown as wind-breaks, fences, and also supplementary fodder sources (S. E. Shackleton & Shackleton, 2018).

Some introduced species also act as hosts of further invasive alien species. For example, in the United States, *Festuca arundinacea* (tall fescue), a cool season-grass introduced from Europe, dominates grasslands and is considered an invasive alien species across multiple states (Barnes *et al.*, 2013; Pfeifer-Meister *et al.*, 2008). The spread of tall fescue is concerning as it also may act as a reservoir host for *Alternaria* (fungal pathogen), which produces crop damaging mycotoxins (H. E. Wilson *et al.*, 2014).

3.3.1.1.4 Agriculture

In a global study of terrestrial plant invasions 407 (46 per cent) of 886 alien plants were introduced intentionally through agricultural pathways (Turbelin *et al.*, 2017). This study reports three of the top five terrestrial invasive alien plant species globally to have their main introduction pathways associated with agricultural practices: *Cyperus rotundus* (purple nutsedge; found in 37 per cent of countries), *Ricinus communis* (castor bean; 31 per cent) and *Leucaena leucocephala* (leucaena; 27 per cent). Agricultural use is also a major source of aquatic plant invasions. In China, several alien freshwater aquatic plants have been introduced for landscaping, water purification and forage purposes, five of which are now considered to be invasive alien species: *Sporobolus alterniflorus* (smooth cordgrass), *Azolla filiculoides* (water fern), *Alternanthera philoxeroides* (alligator weed), *Urochloa brizantha* (palisadegrass) and *Urochloa mutica* (para grass) (Wu & Ding, 2019).

The occurrence of some ungulates as invasive alien species arose from agricultural practices (Spear & Chown, 2009). Farms or hunting of species for fur has resulted in the intentional introduction, or escape from farms or captivity, of: *Mustela vison* (American mink) in Europe (Bonesi & Palazon, 2007; E. J. Fraser *et al.*, 2017); *Procyon lotor* (racoon) in Europe (Beltrán-Beck *et al.*, 2012); *Oryctolagus cuniculus* (rabbits) throughout the world (Lees & Bell, 2008) and particularly in New Zealand (C. M. King & Forsyth, 2021), Australia (Myers *et al.*, 1994) and South America (Howard & Amaya, 1975; Iriarte *et al.*, 2005); *Vulpes vulpes* (red fox) in Australia (Saunders *et al.*, 2010); and *Trichosurus vulpecula* (brushtail possum) in New Zealand (Clout, 2006; C. Jones *et al.*, 2012). **Section 3.3.2.1** on stocking for hunting and **section 3.2.3.3** on pet trade also discuss how these drivers have facilitated invasive alien species.

Agriculture has also facilitated biological invasions by plant and animal pathogens, parasites and diseases. Alien plant pathogens may be introduced *via* seeds and soil used in agriculture (Pimentel *et al.*, 2001). For example, 65 per cent of plant pathogens in the United States were considered alien species (Pimentel *et al.*, 1992), 74 per cent in the United Kingdom (Carlile, 1988), 82 per cent in Australia (Persley & Syme, 1990), 85 per cent in South Africa (Nel, 1983), 74 per cent in India (Singh, 1985), and 75 per cent in Brazil (Echandi *et al.*, 1972). Many microbes and other parasites accompany livestock as they are introduced into new countries (Pimentel *et al.*, 2001). *Mycobacterium bovis* (bovine tuberculosis) was introduced to many places, including New Zealand, as cattle were transported out of Europe during the nineteenth century (N. H. Smith, 2012). In New Zealand, bovine tuberculosis is now also prevalent in other invasive alien species including *Trichosurus vulpecula* (brushtail possum), *Sus scrofa* (feral pig), *Mustela putorius furo* (ferret), *Mustela erminea* (ermine), *Erinaceus europaeus* (European hedgehog) and deer species (Livingstone *et al.*, 2015). In Europe, the introduction of *Procyon lotor* (racoon) also established *Baylisascaris procyonis* (raccoon roundworm), which may potentially induce central nervous system disease in humans (Chinchio *et al.*, 2020).

3.3.1.2 Fragmentation of ecosystems

Increasing exploitation of natural resources and land-use changes have led to widespread fragmentation of terrestrial ecosystems, so that 70 per cent of remaining forest areas globally are now within 1 km distance of a forest edge (IPBES, 2019). Fragmentation is usually associated with loss of total habitat area, changes in habitat quality, and increased biotic and abiotic influence from the surrounding landscape (Eriksson *et al.*, 2002; Sodhi *et al.*, 2010; Vilà & Ibáñez, 2011). Fragmentation of landscapes and habitats is one of the most significant process driving decrease of native biodiversity and species richness globally (IPBES, 2019; Millennium Ecosystem Assessment, 2005b).

Fragmentation increases the proportion of the native habitat exposed to edge effects, where higher propagule pressure and faster growth of pioneer and generalist species, many of which are alien, can drive replacement of native habitat specialists (Laurance & Peres, 2006; Lobo *et al.*, 2011; B. A. Santos *et al.*, 2008; Tabarelli *et al.*, 2008). The increased edge-to-interior ratio of fragmented landscapes increases the prevalence of invasive alien species in fragments, as shown for plant and lepidopteran diversity in South Texas (Stilley & Gabler, 2021), woody plant diversity in New England (J. M. Allen *et al.*, 2013), *Hovenia dulcis* (Japanese raisin tree) in Brazilian Atlantic forest patches (Padilha *et al.*, 2015) and *Sporobolus alterniflorus* (smooth cordgrass) in mangroves along the coast of China (Z. Zhang *et al.*, 2021). Recent studies also document increased spread of invasive alien species in fragmented landscapes over time, such as the study from Achury *et al.* (2021) of *Linepithema humile* (Argentine ant) invading coastal southern California. Similarly, *Ulex europaeus* (gorse) spread widely in fragmented landscapes of south-central Chile while large intact forest areas experienced lower rates of invasion over the same time period (Altamirano *et al.*, 2016).

As fragmentation increases, the remaining fragments are more isolated from each other, which may both promote and hinder biological invasions. Increased patch isolation may promote biological invasions if invasive alien species are more common in the habitats surrounding the patches, as has been shown for alien pasture grasses which frequently occur in Australian forest fragments surrounded by landscapes with high pasture cover (S. Butler *et al.*, 2014). Another example is the prevalence of *Aulacaspis yasumatsui* (cycad aulacaspis scale) on cycads in Guam, where isolated fragments suffered greater damage from these alien scale insects than did fragments with higher connectivity (Marler & Krishnapillai, 2020). Connectivity of native habitats may also be promoting the spread of invasive alien species which are dependent upon native dispersal vector species that depend on this habitat (e.g., Guiden *et al.*, 2015).

Some cases exist in which the fragmented habitat is less favourable to invasive alien species. Insect pests and specialist pathogens of forest trees are less common in counties of the United States which have more fragmented forests (Guo, Riitters, *et al.*, 2018). In the case of animals, patches further apart than the organism is able to cross may hinder the spread of invasive alien species (e.g., Bridgman *et al.*, 2012). The reproductive success of the invasive alien tree *Ligustrum lucidum* (broad-leaf privet) is lower in forest fragments than continuous forests, not due to lower seed production but due to unfavourable soil conditions for seedling establishment in fragments (Aguirre-Acosta *et al.*, 2014). In aquatic environments, artificial fragmentation (e.g., underwater barriers) may slow down the spread of alien species, even though some barriers may be more effective for native species than for alien species (Airoldi *et al.*, 2015).

Fragmentation of native habitat also creates corridors for invasive alien species (**section 3.3.1.3**), increased disturbance (**section 3.3.1.5**) and lower patch habitat quality (**section 3.3.1.6**). A mechanism by which fragmentation promotes biological invasion may be through rendering native populations more vulnerable to local extinction (Hanski, 1999), leaving vacant niches and hence decreasing biotic resistance to invasions and ecosystem resilience (**section 3.4.2**). Most of the evidence for the effects of fragmentation on biological invasions comes from invasive alien plants or plant pest species, and specifically in relation to the spread stage of the biological invasion process (**Chapter 1**, **section 1.4.4**).

3.3.1.3 Creation of anthropogenic corridors

Different types of anthropogenic corridors act as major routes for the transport and spread of invasive alien species (e.g., Galil *et al.*, 2015; Hulme *et al.*, 2008), although these are often not explicitly considered in pathway assessments (CBD, 2014; Leclerc *et al.*, 2018). Anthropogenic corridors, including roads, highways, railways, hiking trails, tunnels, pipelines, power lines, canals and bridges, are rapidly expanding for trade, travel and transport (**sections 3.2.3.1** to **3.2.3.4**). It is projected that length of roads will increase by over 60 per cent (or to between 3 and 4.7 million km) globally from 2010 to 2050 (Dulac, 2013), a large fraction of which is projected to be built in developing countries in some of the world's last remaining wilderness areas, such as the Amazon, the Congo basin and New Guinea (Meijer *et al.*, 2018). The volume of freight transported *via* anthropogenic corridors has consistently grown since the 1960s especially in Europe and North America (**section 3.1.1**; Hulme, 2009a).

Anthropogenic corridors allow both intentional and unintentional transport of invasive alien species, and they create disturbed and transformed habitat such as road and canal verges that allow subsequent establishment and spread of invasive alien species into otherwise impassable regions. The mechanism of the influence of anthropogenic corridors on the stages of the biological invasion process can be summarized as follows; 1) allowing easier transport and spread of invasive alien species by natural (e.g., wind, water, animals) or human mediated (e.g., cars, trains, ships, people) vectors, 2) facilitating establishment of invasive alien species by disturbing, stressing or removing native species and ecosystems along corridor verges, 3) providing new corridor verge habitats for invasive alien species to establish and spread by altering abiotic environmental conditions (e.g., soils, hydrology, wind; Trombulak & Frissell, 2000).

In terrestrial biomes, several global surveys provide evidence that the abundance and diversity of alien plants is higher along roads compared to adjacent native habitat, and decreases with distance away from the roads (Lázaro-Lobo & Ervin, 2019; Suárez-Esteban *et al.*, 2016). The long linear features of roads and railways facilitate the long-distance dispersal of alien seeds (Hulme, 2006). In a selectively logged tropical forest in Bolivia, logging vehicles spread the seeds of the alien *Megathyrsus maximus* (Guinea grass) at least 500 m from the established populations (Veldman & Putz, 2010). Road density and road age also positively correlate with alien species' distributions (Hulme, 2009). For example, alien earthworms have spread farther from older roads in boreal forests of Canada (Cameron & Bayne, 2009), suggesting roads provide fringe sources for colonization of native habitat. Anthropogenic corridors also drastically alter the surrounding biotic, physical and chemical environments. The edges of anthropogenic corridors (e.g., roadsides, highways, railways) provide favourable habitats for the establishment of alien plants (e.g., M. J. Hansen & Clevenger, 2005; Jodoin *et al.*, 2008; Sullivan *et al.*, 2009). Rural roads, mountainside highways and powerlines change the surrounding plant species composition, and enhance the establishment of invasive alien species in mountainous and protected areas (L. G. Anderson *et al.*, 2015; Mortensen *et al.*, 2009; Rentch *et al.*, 2005; Spooner, 2015; Wagner *et al.*, 2014). Some Indigenous Peoples and local communities also observe the role of anthropogenic corridors in facilitating biological invasions, for instance, people in Arunachal Himalayas in India view road construction and road use as the drivers facilitating biological invasion, as well as introduction of cattle which brought alien seeds (Kosaka *et al.*, 2010). In alpine and Arctic ecosystems, the establishment and subsequent spread of alien plants is increased along mountain roads, hiking trails and buried oil pipelines (Alexander *et al.*, 2016; Langor *et al.*, 2014; Liedtke *et al.*, 2020; **section 3.3.5.1**, **Box 3.10**).

In freshwater and marine biomes, canals facilitate the transport, introduction and spread of invasive alien species at global and regional scales (Asth *et al.*, 2021; Bij de Vaate *et al.*, 2002; Boudouresque & Verlaque, 2012). The role of these water corridors in facilitating biological invasions are well studied for fish and aquatic invertebrates (Devin *et al.*, 2005; Karatayev *et al.*, 2008; Rakauskas *et al.*, 2016), especially in Europe (e.g., Katsanevakis *et al.*, 2013). For example, 507 marine alien species have arrived in European Seas through canals, such as the Suez Canal (**Box 3.7**; Katsanevakis *et al.*, 2013). Since the eighteenth century, the connection of the European seas and rivers to the Eurasian waterways *via* canals showed a stepwise increase, and the extensive network of inland waterways has allowed the biological invasion of aquatic alien species from different biogeographical regions (Leuven *et al.*, 2009), such as the establishment of Ponto-Caspian invertebrates throughout the central European corridors (Karatayev *et al.*, 2008). Another example is the shipping canals near Chicago, Illinois that link the Great Lakes with the Mississippi River, which have allowed the exchange of 15 species of fish and invertebrates formerly confined to just one of the basins (Rahel, 2002). Additionally, inter-basin water transfers provide a direct link between previously isolated catchments and thereby modify the water flow, chemistry and temperature of receiving waters. Water inflow *via* canals can result in eutrophication and changes in salinity, thereby allowing the establishment of invasive alien species (e.g., Pienimäki & Leppäkoski, 2004; Sarà *et al.*, 2018).

Thus, creation of anthropogenic corridors is an important driver across all stages of the biological invasion process (transport, introduction, establishment and spread) for various taxa (e.g., plants, vertebrates and invertebrates) in terrestrial, freshwater and marine biomes.

Box 3 7 **The Suez Canal and invasive alien species.**

The Suez Canal, a linchpin of transportation networks between Europe and Asia, carries over 10 per cent of global trade, with19,000 vessels transiting the Canal in 2020 (Veiga, 2021). The Canal is also the main pathway of alien species introduction into the Mediterranean Sea. The Suez Canal was opened over 150 years ago, yet Erythraean species are newly recorded in the Mediterranean to this very day **(Figure 3.16)**. Biological invasions by Erythraean species are driven by the region's environmental characteristics and anthropogenic activities. The latter include: physical changes to the Canal that have impacted its hydrography and hydrology, and increased its potential as a "corridor"; and changes to the Levantine marine environment that have made it more susceptible to biological invasion by modifying its hydrological properties and species diversity, and destabilizing the shelf community structure (Galil, 2006).

The Suez Canal (8 m deep, with cross-section area 304 m^2, when built in 1869) is hydrographically complex, passing through five anthropogenic lakes of widely diverse salinity (Menzalah, Ballah, Timsah, Large and Small Bitter Lakes). The dissolution of the Bitter Lakes' salt bed, complete by the 1960s, removed the early Canal's salinity barrier. A recent study of the Canal's flow intensity and direction (1923–2016) supports unidirectional biological invasions into the Mediterranean, with significant increase in northward flow during the early 1980s following a major expansion (depth from 15.5 to 19.5 m, doubling cross-section area), and a second expansion in 2015 after the opening of the "new" Suez Canal (Biton, 2020). A larger Canal accommodates transit of more and larger vessels, many in ballast and befouled, and discharges a larger volume of Red Sea waters with their entrained biota into the Mediterranean Sea.

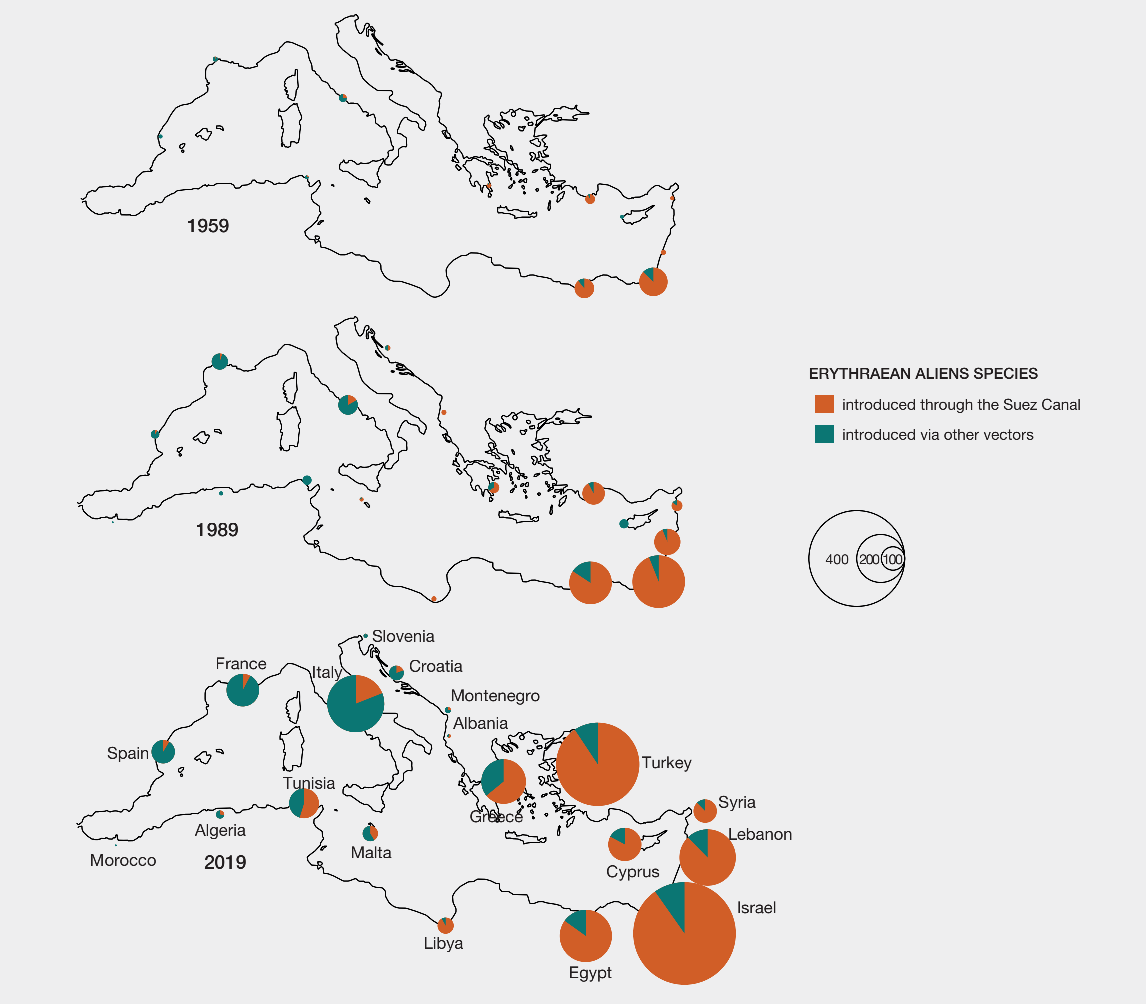


Figure 3 16 **Number of multicellular marine alien species in peri-Mediterranean countries, and their means of introduction, 1959, 1989, 2019.**

Lighter tone: Erythraean aliens (i.e., introduced through the Suez Canal), darker tone: alien species introduced *via* other vectors. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7861139

3.3.1.4 Deployment of marine infrastructure

Coastal landscapes are being transformed through marine urban sprawl with an increase in construction of artificial structures to support commercial, residential and tourist activities (Dafforn *et al.*, 2015; Bulleri & Chapman, 2010). Indeed, more than 50 per cent of the shorelines of some regions of Europe, United States, Australia, and Asia are modified by hard engineering. Offshore aquaculture facilities and offshore energy infrastructures are also increasing in prevalence. Marine urbanization is predicted to escalate in the future as sea-level rises and extreme climate events, including storms, increase in frequency (Dafforn *et al.*, 2015). Artificial structures alter seascapes and the functioning of marine ecosystems through local and regional effects (Bulleri & Chapman, 2010; Todd *et al.*, 2019) including the establishment and spread of invasive alien species.

The potential for invasive alien species to utilize marine infrastructure is widely recognized (Bulleri & Chapman, 2010; Bulleri & Airoldi, 2005; Vaselli *et al.*, 2008). Marine infrastructure can facilitate invasive alien species by providing artificial hard substrates that some invasive alien species can colonize (Farr *et al.*, 2021). Indeed, artificial hard structures such as breakwaters, jetties, seawalls, floating pontoons and pier pilings provide suitable habitats for alien species (Bulleri & Airoldi, 2005; S. L. Williams & Smith, 2007) and can also function as corridors through unsuitable habitats (Bulleri & Airoldi, 2005). Nearshore infrastructure is considered to provide entry points for invasive alien species, with the numbers of invasive alien species on pontoons and pilings being 1.5-2.5 times higher than on natural rocky reefs (Glasby *et al.*, 2007). *Codium fragile* (dead man's fingers), an invasive alien seaweed species native to east Asia, colonized hard structures installed to provide coastal protection in the northern Adriatic Sea and is now found on temperate rocky shores around the world (Bulleri & Airoldi, 2005), and has also replaced native kelp on the leeward shores of the United States (Levin *et al.*, 2002). Similarly, a study on invasive alien ascidians demonstrated that ascidian species spread onto natural habitats from marine infrastructure, and that species differ in the rate and success of this secondary spread (Simkanin *et al.*, 2012). In a global literature survey, the alien ascidians *Botrylloides violaceus* (violet tunicate) and *Botryllus schlosseri* (star ascidian) were reported four times as often in anthropogenic marine habitats relative to natural habitats, while two other alien ascidians, *Didemnum vexillum* (carpet sea squirt) and *Styela clava* (Asian tunicate), were encountered on floating docks, pilings and aquaculture installations eight times as often as they were found in nearby natural habitats (Simkanin *et al.*, 2012). These findings illustrate the differences in biological invasion potential and/or rate between closely related species.

Offshore floating structures, such as wind facilities, can provide substrate for introduced hard-substrate benthic organisms to colonise, and thus can contribute to the further spread of invasive alien species, especially in the intertidal zone (Kerckhof *et al.*, 2016). Deepwater and offshore floating infrastructures generally are considered less likely to be colonized by invasive alien species than nearshore infrastructures (Farr *et al.*, 2021) because the nearshore is often associated with higher human activity and consequently increased pathways of introduction in comparison to offshore locations.

3.3.1.5 Changes in landscape-seascape disturbance regimes (intensification and reduction)

Changes in landscape-seascape disturbance regimes, including both intensification and reduction in disturbance intensity, have been ubiquitous in natural ecosystems as a result of human activities; for example over 50 per cent of the global land area has experienced changed fire regimes, and fires are expected to become more common in coming decades as a result of climate change and increasing human occupation (IPBES, 2018b). Such changes may affect the capacity of invasive alien species to establish and thrive through direct effects of changes in disturbances. Effects may also be more indirect, through interfering with native competitors, grazers, or predators, or through the modification of fire frequencies or nutrient and water regimes (**sections 3.3.4.5**, **3.3.3.1** and **3.3.1.5** respectively). At broader spatial scales, changes in landscape-seascape disturbance regimes may affect invasive alien species through fragmenting landscapes, creating corridors, the deployment of infrastructure, or degrading habitats, but also through protecting areas from disturbance, for example in designated protected areas (**sections 3.3.1.2** to **3.3.1.5**).

In an observational study spanning 200 sites around the world, disturbance *per se* was found to be a weak predictor of plant invasions (Moles *et al.*, 2012). An older literature survey (Lozon & MacIsaac, 1997) found a greater importance of disturbance for successful plant invasions (implicated in 67 per cent of disturbance caused by invasive alien species) than by animals (implicated in 28 per cent of disturbance caused by invasive alien species), particularly during the establishment phase (86 per cent vs. 12 per cent relied on disturbance for plants vs. animals). The role of landscape disturbance in influencing microbial invasive alien species is far less understood than for macro-organisms, but the literature that exists suggests patterns remain similar with sites of high disturbance, anthropogenic impact, fluctuating resource supplies and release from predators resulting in increased establishment of invasive alien microbial species (Litchman, 2010). Overall, increased landscape disturbance *per se* hence seems to have a weak but positive role in facilitating invasions.

A more nuanced analysis focusing on changes in disturbance regimes, however, can provide better predictive power than disturbance regime *per se*. Several reviews have found that changes in land-use regimes, and in particular in human-mediated disturbance regimes related to fire, grazing and agriculture, facilitate plant invasions through both direct and indirect pathways (Jauni *et al.*, 2015; Moore, 2005; Vilà & Ibáñez, 2011). Experimental studies support these observations, frequently indicating that changes to disturbance regimes, both increases and decreases in disturbance frequency and intensity relative to natural or historic levels, and in particular the introduction of novel disturbance types, provide opportunities for alien plant species to establish (Kempel *et al.*, 2013). **Sections 3.3.1.5.1**, **3.3.1.5.2** and **3.3.1.5.3** therefore summarize the ways in which changes, and particularly intensification of human disturbance regimes, increase the establishment and spread of invasive alien species. There is stronger evidence for disturbance effects on terrestrial systems and plants than other systems and taxonomic groups, but some evidence also exists from aquatic and marine systems and for vertebrates, invertebrates and microorganisms. All IPBES regions are represented, with much of the evidence from Australia and the United States. The literature on disturbance regimes as a driver that facilitates invasive alien species covers all stages of the biological invasion process, but with more evidence on the establishment and spread stages, the latter often associated with documentation of the impact on native biodiversity and human livelihoods (**Chapter 4**).

3.3.1.5.1 Agricultural disturbance regimes

In terrestrial biomes, a global meta-analysis (Jauni *et al.*, 2015) found that plant invasions can be facilitated by discrete disturbance events such as fire, agricultural activity, and more generally broad shifts in anthropogenic activity. Specifically, they found that increased domestic grazer activity and general anthropogenic disturbance events increased both the diversity and abundance of alien species, whilst fire- or soil-based disturbance activities led only to increases in diversity of alien species. This trend was stronger in forest ecosystems than in wetlands and grasslands. Importantly, time elapsed since the disturbance occurred was considered critical, with significant responses only observed in cases where communities were monitored more than five years post-disturbance. In line with these findings, in Ghana, conversion to maize production resulted in increasing removal of fallow trees, which has encouraged land degradation and facilitated establishment and spread of *Chromolaena odorata* (Siam weed; Amanor, 1991). In arid and semi-arid rangelands of the United States, livestock overgrazing decreases the plant cover of native palatable grasses and accelerates the dominance of alien annual grasses (e.g., *Bromus tectorum* (downy brome); Chambers *et al.*, 2007; Keeley *et al.*, 2003). In the grasslands of the Austral Andean Mountains in Argentina, establishment of the invasive alien *Pinus halepensis* (Aleppo pine) was considerably higher in areas grazed by feral horses, where perennial grasses were negatively affected by defoliation, giving advantage to the alien plant *Echium plantagineum* (Paterson's curse) (de Villalobos & Schwerdt, 2020; de Villalobos & Zalba, 2010). In Australia, overgrazing by introduced feral camels, buffalo and pigs has facilitated invasive alien species establishment in arid and semi-arid ecosystems throughout the country (Burrows, 2018; Sloane *et al.*, 2021). Invasive alien plants often have higher performance and higher resource use efficiency than coexisting native species, suggesting a higher ability to benefit from increased resource availability resulting from changes in disturbance regimes as a potential mechanism (e.g., Daehler, 2003; Kolar & Lodge, 2001; Leishman & Thomson, 2005). Among animals, *Solenopsis invicta* (red imported fire ant) was characterized as a "disturbance specialist" when subjected to mowing and ploughing regimes, to the extent that the species was found not to invade forest habitats of native ants in the absence of such disturbances (J. R. King & Tschinkel, 2008). Increasing agricultural disturbance also benefited alien predatory *Coccinellidae* (ladybeetles) in Chile, and these alien ladybeetles could be considered "disturbance specialists" (Grez *et al.*, 2013). Modified landscapes may also support higher abundances of invasive alien animals than unmodified landscapes, for example introduced *Vulpes vulpes* (red fox) thrive within Australian agricultural systems (Graham *et al.*, 2012; Towerton *et al.*, 2011).

Biological invasions in terrestrial systems may be affected by land abandonment as well as land-use intensification. After abandonment, the succession from agricultural to forested landscapes is generally associated with an increased spread in plant invasions, particularly after crop abandonment (Vilà & Ibáñez, 2011), which may be linked to higher competitive ability and hence establishment and spread of some invasive alien species under the reduced disturbance intensity and frequency in post-abandonment vegetation (van der Zanden *et al.*, 2017). The role of abandonment in facilitating invasive alien species is well known among Indigenous Peoples and local communities in several parts of the world. In the Panchase area of Nepal, Indigenous communities report that land-abandonment has led to the establishment and spread of invasive alien species (Schwilch *et al.*, 2017). In the Amatole District of the Eastern Cape, South Africa, local communities noticed that the abandonment of arable fields coupled with the dispersal of seeds by local birds have led to invasion by *Lantana camara* (lantana; Jevon & Shackleton, 2015). Indigenous Peoples and local communities in South Africa have also observed that some abandoned agricultural lands can become hotspots of invasive alien species (C. M. Shackleton & Gambiza, 2008).

3.3.1.5.2 Changes to fire regimes

Fire is a key natural disturbance process that plays an important role in regulating community composition and ecosystem functioning in a diversity of ecological systems worldwide (He *et al.*, 2019; Keeley *et al.*, 2011; Pausas & Keeley, 2019). In fire-adapted systems, continuation of the historic natural or anthropogenic fire regimes generally has relatively little influence on either native species performance or the establishment of alien species whereas loss of traditional fire regimes may benefit invasive alien species (Alba *et al.*, 2015; L. T. Kelly *et al.*, 2020; Velle *et al.*, 2014). A meta-analysis of the role of fire on native and invasive alien species found that prescribed low-intensity burns may benefit native species but generally do not affect alien species, whereas wildfires consistently enhanced alien species performance and diversity, and especially so in arid shrublands, temperate forests and heathlands (Alba *et al.*, 2015). The evidence from this global study was largely from the United States and Australia, pointing to regional knowledge gaps. Invasive alien species may benefit from both reduction and enhancement of fire regimes relative to historic levels. For example, in naturally fire-prone prairies in the United States, fire suppression led to the dominance of invasive alien earthworms (Callaham *et al.*, 2003; Callaham & Blair, 1999), and increased frequency or intensity of fire relative to historic fire regimes tended to increase diversity and performance of alien plants, whereas native biodiversity was highest when historic fire regimes were maintained (D'Antonio, 2000). In tussock grasslands in New Zealand, alien spiders were more successful at colonizing after burning, which provided an initial advantage in resource competition for these invasive alien arthropods (Malumbres-Olarte *et al.*, 2014). Intensified fires along with overgrazing led to the loss of fire-intolerant trees and shrub species and facilitated the establishment of the alien grass *Bromus tectorum* (downy brome) in shrublands and increased establishment and spread of invasive alien species in coniferous forests (Chambers *et al.*, 2007, 2014; Keeley *et al.*, 2003; Roundy *et al.*, 2014).

Some invasive alien species not only benefit from modified fire regimes, but once established, may in turn further modify fire behaviour and community composition (Grace *et al.*, 2001). For example, some alien species increase the fuel load or flammability of the ecosystem, resulting in increased fire frequency or intensity (Brooks *et al.*, 2004; Mandle *et al.*, 2011). Alternatively, burned environments may be more susceptible to biological invasion by species with fire specific traits, such as seed release contingent upon fire or smoke (Franzese & Raffaele, 2017; Gaertner *et al.*, 2014). In many cases, fire primarily influences native and alien animal species through effects on vegetation structure and composition. For example, within Australian tropical savannahs, invasive alien predators such as feral cats, dingoes and snakes may be attracted to burnt landscapes, where they may hunt more effectively (Lozon & MacIsaac, 1997; H. W. McGregor *et al.*, 2014, 2016). In Australian forests, prescribed forest fires reduced understory cover by more than 80 per cent and the occurrence of invasive alien predators increased five-fold, whereas medium-sized native mammalian prey were disadvantaged (Hradsky *et al.*, 2017). Climate and land-use change are now driving changes in global fire regimes, pointing to potentially important interactive effects (**section 3.3.4**).

3.3.1.5.3 Aquatic and marine disturbance regime changes

The biological invasion of aquatic alien species may be facilitated through land-use intensification in the watershed. There is an increased likelihood of invasive alien species establishing within impacted watersheds where increased sedimentation, altered flow rates, increased pollution and habitat destruction lower intrinsic biotic resistance (Havel *et al.*, 2015). In New Zealand braided river systems, alien and native aquatic plants respond to different drivers of change in nature, and in particular disturbances to flow regimes. For example, winter flow variability may increase alien species, while flow stabilization may promote coverage of such species (Brummer *et al.*, 2016). Regulated flow regimes, including floods, also mediate invasive alien plants in the Australian Murray-Darling river catchments (Catford *et al.*, 2011, 2014), with impacts mediated by seasonality along with species' life-history strategies (Greet *et al.*, 2013). In China, the rate of onward spread and establishment of *Lithobates catesbeianus* (American bullfrog) from the points of introduction (for aquaculture) throughout the local watershed was facilitated by native habitat loss and land-use change (X. Wang *et al.*, 2022). In the Mediterranean Sea, fish overgrazing and sediment disturbance caused by vessel anchoring decrease the resistance of native seagrass beds, and thereby allow the establishment and spread of invasive alien *Caulerpa racemosa* (green algae; Tamburello *et al.*, 2014). In Italy, however, clearance of seagrass *Posidonia oceanica* (Neptune grass) led to a reduction in the apparent ecological resistance towards the *Caulerpa cylindracea* (green algae) invasion (Casoli *et al.*, 2021; Marín-Guirao *et al.*, 2015).

3.3.1.6 Landscape and seascape degradation

Anthropogenic degradation of terrestrial ecosystems occurs in nearly all types of landscapes around the world, although there are no consistent global figures about the extent of this phenomenon (IPBES, 2018b). Landscape and seascape degradation involves many processes that drive the decline of biodiversity and ecosystem functioning, and in some cases nature's contributions to people in many parts of the world (IPBES, 2018b; Millennium Ecosystem Assessment, 2005a; United Nations Convention to Combat Desertification, 2017). This section summarizes the roles of desertification, soil/water salinization, soil/water erosion and soil/water acidification in affecting biological invasions.

Land degradation related to desertification is a pervasive global phenomenon in arid and semiarid ecosystems subjected to overgrazing (**section 3.3.1.5**), fire (**section 3.3.4.5**) and drought (**section 3.3.4.2**). Separating out the influence of land degradation *per se* from other interlinked drivers responsible for biological invasions is difficult (IPBES, 2018b; Ravi *et al.*, 2009). Acceleration of soil erosion due to agriculture and mismanagement is widely reported, especially from Asia, Latin America and Africa (FAO, 2015; IPBES, 2018b). Soil erosion can increase the establishment of alien species, as exemplified by annual *Bromus* grass in arid and semiarid grasslands of the United States (Germino *et al.*, 2016).

Additionally, invasive alien species may be intentionally introduced to restore degraded land, for example Indigenous Peoples and local communities report the intentional introduction of invasive alien species to manage land degradation (**section 3.2.5**, **Box 3.6**). Stress-tolerant alien plants are often planted in degraded areas for ecosystem restoration (**Glossary**), and can spread from the planted areas (Hobbs *et al.*, 2006), for instance, alien grasses (e.g., *Bromus tectorum* (downy brome)) seeded for preventing soil erosion in degraded grasslands or for livestock forage in overgrazed rangelands (D'Antonio & Meyerson, 2002; D'Antonio & Vitousek, 1992) and alien trees have been planted to stabilize riparian zones. Irrigated land damaged by salinization is estimated globally to be 60 million ha (FAO, 2015; IPBES, 2018b; Squires & Glenn, 2011). Soil salinization associated with waterlogging leads to the replacement of pre-existing native perennial herbaceous plants with salinity-tolerant alien annual plants in southern Australia (Hobbs *et al.*, 2006).

Especially in North America, Europe and Australia, estuarine and coastal areas have been dramatically transformed over the past 150 to 300 years. Degradation linked to industrialization/urbanization (**sections 3.2.2.4** and **3.3.1.4**) has resulted in accelerated establishment and spread of invasive alien species in once diverse and productive areas (Lotze *et al.*, 2006). For example, creation of a metropolitan coastal front in Athens and the Piraeus port led to the occupancy of an alien scleractinian coral, *Oculina patagonica*, in shallow coastal habitats of the Mediterranean Sea (Salomidi *et al.*, 2013). Overexploitation, pollution, disease and climate change are causing global declines of coastal lagoons and coral reefs, especially on the Great Barrier Reef (IPBES, 2018d). There however seems to be clear evidence that coastal disturbance (e.g., harbour constructions) could be a driver facilitating biological invasions (Boudouresque & Verlaque, 2012; J. Klein *et al.*, 2005).

In aquatic systems, invasive alien species may become more prevalent as construction of water storage infrastructure increases (**section 3.3.1.4**), and in many cases, the mechanisms are linked to changes in disturbance regimes. Features such as reservoirs may act as stepping stones for invasive alien species by providing a homogenous, species-poor, early successional habitat providing little biotic resistance for initial occupation (Havel *et al.*, 2005, 2015; **section 3.4.2**). In the Laurentian Great Lakes region of Wisconsin, United States, Johnson *et al.* (2008) found dams and impoundments to be a significant predictor of occurrence for the invasive alien species *Bythotrephes longimanus* (spiny water flea), *Dreissena polymorpha* (zebra mussel), *Osmerus mordax* (rainbow smelt), *Orconectes rusticus* (rusty crayfish) and *Myriophyllum spicatum* (spiked watermilfoil) – ranging between 2.4 to 300 times more likely to occur in impoundments than natural lakes, even after taking into account other environmental and anthropogenic factors. In the same systems, impoundments were also more likely to support multiple invasive alien species (P. T. Johnson *et al.*, 2008).

3.3.2 Direct exploitation of natural resources

Direct exploitation of natural resources includes both the exploitation of biotic resources through species harvesting (**section 3.3.2.1**) as well as of abiotic resources such as water (**section 3.3.2.2**) and mining for minerals and fossil fuels (**section 3.3.2.3**). These changes are closely linked with major economic (**section 3.2.3**) and demographic (**section 3.2.2**) indirect drivers of change in nature and may lead to a range of wider ecosystem impacts, including habitat degradation and loss as well as changes in landscape and seascape disturbance regimes (**section 3.3.1**). Section 3.3.2 thus describes evidence for links between the extraction of specific resources and invasive alien species **(Figure 3.17)**, and makes reference to other indirect and direct drivers when relevant. The demographic and economic background of these changes are described in **section 3.2** and consequences of land degradation more generally is described in **section 3.3.1**.

3.3.2.1 Species harvesting

Globally, the extraction of biological resources for human use for food, fibre and fuel has doubled since 1970, now constituting more than 22 billion tonnes per year (IPBES, 2019). The livelihood of over 350 million people depends on the extraction of non-timber forest resources, and over six million tons of medium to large wild animals are harvested every year in the tropics, where they are often an important food source (IPBES, 2019). Both terrestrial and freshwater ecosystems are affected by species harvesting in different ways. About 50,000 wild species are harvested for food, energy, medicine, materials, income generation, or other uses globally, and an assessment of 10,098 species

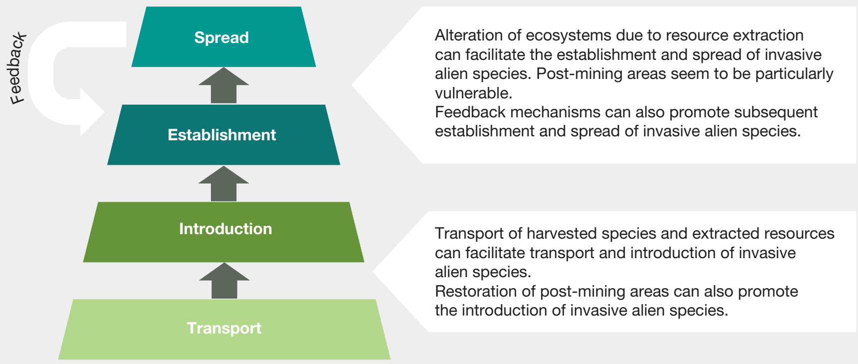


Figure 3 17 **Examples of the role of direct exploitation of natural resources as a driver facilitating invasive alien species across stages of the biological invasion process.**

Transport of harvested species and efforts to restore degraded areas are examples of activities that can lead to the transport and introduction of alien species, the on-site activities related to extraction can facilitate establishment and spread. Introductions of alien species for harvesting often occur at a massive scale, increasing the risk of feedbacks facilitating further introductions.

across 10 taxonomic groups shows that at least 34 per cent are used sustainably, whereas unsustainable harvesting contributes towards elevated extinction risk for 28-29 per cent of near-threatened and threatened species (IPBES, 2022c).

The loss of native biomass and biodiversity in an ecosystem through harvesting has been directly and indirectly linked to increased susceptibility to biological invasions by a wide range of alien species and in a wide range of terrestrial and aquatic environments (IPBES, 2022c; Iverson *et al.*, 2019; Kota *et al.*, 2007; Rebbeck *et al.*, 2017; Schrama & Bardgett, 2016). Many studies of the role of overharvesting on the success of invasive alien species explore indirect effects through trophic changes (Barrios-O'Neill *et al.*, 2016; Kota *et al.*, 2007; Rand & Tscharntke, 2007). For example, an extensive study in the Mediterranean Sea shows that the loss of predators through overfishing resulted in an increase in alien invertebrates in the prey fauna (Rilov *et al.*, 2018). Success of invasive alien species and their impacts may vary, however, depending on whether the harvested native predators are generalists or specialists, and on the intensity and nature of the interaction (Rand & Tscharntke, 2007; W. E. Snyder & Evans, 2006; Tylianakis *et al.*, 2008). Loss of hunted and fished native species may also motivate the release of alien species as alternative species for harvest, as discussed below for terrestrial and aquatic settings.

3.3.2.1.1 Introduction of game for hunting

Stocking of game for hunting purposes is a common practice in many parts of the world, for both recreational and subsistence uses (**section 3.2.1**, **Box 3.2**), and can be an important driver facilitating invasive alien species in many different contexts. A European study (Carpio *et al.*, 2017) found stocking for hunting to be a dominant source of mammal introductions (24 per cent of all known introductions) and birds (30 per cent). Similar patterns were observed in Latin America, where 39 per cent and 22 per cent respectively, of the introduced mammals (69 species in total) and birds (62 species), were introduced intentionally for hunting purposes, compared to an overall 11.2 per cent for food and feed, 5.3 per cent for biological control, and 4.2 per cent for fur industry (Carpio *et al.*, 2020). In the United States, game ranches are also sources of invasive alien species (Geist, 1985). Common alien species introduced for sport or game hunting include: deer species in New Zealand (C. M. King & Barrett, 2005), Australia (N. E. Davis *et al.*, 2016), Latin America (Petrides, 1975) and Europe (Carpio *et al.*, 2017); *Sus scrofa* (feral pig) native to Eurasia and now present on all continents but Antarctica, along with many oceanic islands (Barrios-Garcia & Ballari, 2012; Long, 2003); and various bird species such as pheasants (Blanco-Aguiar *et al.*, 2008) and *Anas platyrhynchos* (mallard) in Australia, New Zealand, South Africa and Hawaii (Rhymer *et al.*, 1994; Fowler *et al.*, 2009; Guay & Tracey, 2009; Government of the Republic of South Africa, 2016). Attempts to control invasive alien species introduced for hunting using biological control have led to further biological invasions, for example the introduction of mustelids to control rabbits and hedgehogs to control garden pests in New Zealand (C. M. King & Forsyth, 2021).

3.3.2.1.2 Introductions of aquatic and marine species for fisheries and angling purposes

Intentional release of fishes and other marine organisms into rivers, lakes and seas to enhance recreational fishing as well as livelihoods is both widespread and common (**section 3.2.1**). These introductions can be distinguished from those linked to aquaculture by being intentionally released into the wild, although the high permeability of aquaculture installations suggests the distinction is somewhat arbitrary (**section 3.3.1.1.1**, FAO, 1995; Grosholz *et al.*, 2015). Globally, hatchery-reared juveniles of more than 180 species of fish and shellfish have been released in the wild for various purposes, including replacing locally extinct stocks (restocking), augmenting a viable fishery (stock enhancement) and creating new fisheries (sea ranching) (Bartley & Bell, 2008; Kitada, 2018; Q. Wang *et al.*, 2006). As many of these releases are occurring at massive scales either outside the native distribution of the species or facilitating spread outside the native range, this constitutes a substantial pathway for aquatic introductions. Introductions, unintentional as well as intentional (e.g., live bait) and legal as well as illegal, have led to the establishment and spread of alien species in freshwater systems in Europe, North America, South America, South Africa and Oceania (Britton & Orsi, 2012; Cambray, 2003; Carpio *et al.*, 2019; Cerri *et al.*, 2018; A. J. S. Davis & Darling, 2017; Ellender & Weyl, 2014; Gherardi *et al.*, 2009; Lintermans, 2004; V. R. Ribeiro *et al.*, 2017; E. R. C. Smith *et al.*, 2020; M. R. Snyder *et al.*, 2020; Weyl *et al.*, 2020). In the Mediterranean basin alone, stocking (for angling, commercial purposes, or biological control) is implicated in over 35 per cent of more than 500 documented freshwater fish introductions (Tricarico, 2012). In the Arctic, *Paralithodes camtschaticus* (red king crab) was intentionally introduced from the Sea of Okhotsk to the Barents Sea in the 1960s to establish a new commercial fishery, and it is currently established and is spreading to the extent that it is commercially harvested by Russian and Norwegian fisheries (Hindar *et al.*, 2020). *Oncorhynchus gorbuscha* (pink salmon) was introduced to several rivers in North-west Russia in the 1950s, and while the first return to rivers in Russia and Northern Norway was recorded in the 1960s, a self-sustaining population did not establish until several decades later. From 2017 onwards, rapid establishment and spread occurred, to the extent that the pink salmon was a dominant fish species in several rivers in Northern Norway in 2021 (with up to 23-fold increase in population size from 2019-2021), and it had spread along the entire Norwegian coast (Berntsen *et al.*, 2022; Hindar *et al.*, 2020).

A compelling example of the cascading effect of species harvesting is the loss of almost 200 species of endemic cichlids following overfishing and introduction of the predatory alien fish *Lates niloticus* (Nile perch) into Lake Nabugabo and Lake Victoria in Africa (Bwanika *et al.*, 2006; Rahel, 2002). Both overharvesting of native species and altered abiotic conditions allowed alien fishes to become established in the lakes, which then eliminated the native species through competition or predation (B. E. Marshall, 2018; Rahel, 2002). The cascade of ecological interactions leading to the demise of native fish in Lake Victoria started with overfishing in the first half of the twentieth century (Aloo *et al.*, 2017), followed by a series of introductions of the invasive alien fish *Lates niloticus*. The *Lates niloticus* population in Lake Victoria peaked at around 2.3 million tonnes in 1999, when it accounted for 92 per cent of the total fish biomass, but fell to less than 300 000 tonnes in 2008, of which the majority were below the required length for export. *Lates niloticus* has subsequently depleted its native prey, hypochromine cichlid fishes (IPBES, 2019), and unsustainable fishing in the lake continued (Luomba, 2016). This top-down cascade led to profound changes in the lake ecosystem, resulting in further reduction in population size and extinction of a number of endemic fishes (**Chapter 4**, **Box 4.10**; B. E. Marshall, 2018).

3.3.2.2 Hydrological resource harvesting

Global water use has increased six-fold over the last 100 years and recent increases in water use have been at a rate of 1 per cent per year (United Nations, 2020). This increasing water use has required large investments in infrastructure, including 50,000 dams and over 16 million reservoirs worldwide (IPBES, 2019), as well as extensive extraction of groundwater resources (International Groundwater Resources Assessment Centre, 2018). There is an increasing recognition that human-mediated hydrological disturbances directly or indirectly facilitate plant and animal invasions (Brummer *et al.*, 2016; Richardson, Holmes, *et al.*, 2007; Truscott *et al.*, 2006). As many alien species thrive in low-competition environments created by hydrological disturbances, biological invasions are often positively associated with the level of hydrological and other disturbances (M. A. Davis *et al.*, 2000; Ricciardi *et al.*, 2017).

Damming and channelization of freshwaters (streams and rivers) and their associated reservoirs can facilitate biological invasions through several mechanisms. First, hydrological alterations through dam constructions may act as reservoirs for invasive alien species and create new habitats which may be colonized by invasive alien species (Richardson, Holmes, *et al.*, 2007). Second, water diversions create new hydrological connections that can facilitate the transfer of a broad suite of aquatic species (including invasive alien species) into new regions. For example, the Chicago Area Waterway was constructed more than 100 years ago to connect Lake Michigan and the Mississippi River, and has permitted invasive alien species to move south from the Great Lakes, and may allow invasive alien *Hypophthalmichthys molitrix* (silver carp) and *Hypophthalmichthys nobilis* (bighead carp) to spread in the opposite direction (e.g., Jerde *et al.*, 2013). Similarly, the water supply to both Los Angeles and San Diego from the lower Colorado River below Lake Mead has been colonized by the biofouling *Dreissena rostriformis* *bugensis* (quagga mussel; e.g., Hickey, 2010). Further, the South-to-North Water Transfer Project, which diverts water from the Yangtze River to northern China, is predicted to promote the further spread of an array of aquatic invasive alien plants, including *Alternanthera philoxeroides* (alligator weed), *Pontederia crassipes* (water hyacinth) and *Pistia stratiotes* (water lettuce) into northern waterbodies (D. Liu *et al.*, 2017).

Hydrological resource use that causes periodic rise and fall of (surface and ground) water levels can make space and resources available for invasive alien species to establish and spread in aquatic and adjacent terrestrial habitats. An example is the invasions of African grasses, including *Melinis minutiflora* (molasses grass), in waterlogged Neotropical savannahs which were driven by changes in the groundwater depth from hydrological disturbance (Xavier *et al.*, 2017). Once an invasive alien species establishes, positive feedback mechanisms, occurring *via* biotic facilitation by the invasive alien species (**section 3.3.5.1**), can promote subsequent biological invasions and promote further spread of invasive alien species, as has been observed for riparian habitats in Czech Republic in which an invasive plant, *Heracleum mantegazzianum* (giant hogweed), resulted in extensive spread in adjacent terrestrial landscapes (Pyšek *et al.*, 2008).

Hydrological alterations or disturbance (e.g., water abstraction) sometimes occur concurrently with other altered habitat conditions (e.g., dryness, salinization, erosion and land and sea degradation) that also favour the introduction and further establishment of invasive alien species. Such alterations in aquatic habitat have favoured establishment of invasive alien species such as *Dreissena polymorpha* (zebra mussel) and *Potamocorbula amurensis* (Amur River clam) in high numbers, with negative consequences for many pelagic and benthic fauna species, especially native mussels in those ecosystems (Grosholz, 2002).

3.3.2.3 Mining (minerals, metal, fossils fuels)

Mining for minerals, metals, oil and other fossil fuels is driven by the energy demands of modern society (Ali *et al.*, 2017) and the transport of these materials accounts for 30 per cent of maritime traffic (IUCN, 2020) contributing to 60 per cent of global GDP (IPBES, 2019). Resource extraction activities also assist in the introduction of invasive alien species to new locations. While mining has a relatively small contribution to overall land-use change (less than about 1 per cent of the area; Maus *et al.*, 2020), its ecological footprint is large (Sonter *et al.*, 2014).

The transport of equipment, the construction of roads or harbours to access mining sites, and the associated increase in vehicles or ships for construction of infrastructure and for transport of mining products can act as pathways and vectors for the introduction of invasive alien species and pathogens, while also facilitating the establishment and spread of invasive alien species due to increased disturbance (F. Bell & Donnelly, 2006; Gelbard & Belnap, 2003; **sections 3.3.1.3**, **3.3.1.4**, **3.3.1.5** and **3.3.1.6**). For example, vehicles and road drainage assisted in the dispersal of spores of *Phytophthora lateralis*, an alien root disease, known to infect the native *Chamaecyparis lawsoniana* (Port Orford cedar) in coal mining areas in the United States (Zobel *et al.*, 1985). Similarly, the introduction of marine invasive alien *Tubastraea* spp. (sun corals) to Brazil was associated with towing and anchoring of oil platforms in coastal waters (Capel *et al.*, 2019). The disturbance and disruption to landscapes caused by mining and resource extraction creates suitable habitats for alien grasses, shrubs and trees to establish and spread (Franklin *et al.*, 2012; Lemke *et al.*, 2013). This can occur across several different types of mining such as coal bed mining (Bergquist *et al.*, 2007; Oliphant *et al.*, 2017), open pit mines (Hou *et al.*, 2019) and fossil fuel extraction activities (Butt *et al.*, 2013). In the context of mining, increased abundance of established invasive alien species are associated with disturbed and fragmented of habitats, the removal of native vegetation cover or through the altered soil nutrients from mine-water discharge (Bergquist *et al.*, 2007).

Mining increasingly tends to occur in remote and previously undisturbed areas (Butt *et al.*, 2013), which may enhance the potential contribution of mining to invasive alien species colonization and establishment in new areas globally. For example, there has been a significant increase in the exploration of oil and gas in marine environments (Jouffray *et al.*, 2020), particularly in Africa (G. Zhang *et al.*, 2019) and the Arctic and Antarctic regions (Petrick *et al.*, 2017), increasing the risk of biological invasions in the marine realm, across multiple taxa, from shipping (Seebens *et al.*, 2013) and discharges of ballast water (Holbech & Pedersen, 2018). Multiple regions and ecosystems across the world are at risk of increased mining activity, including forests (Macdonald *et al.*, 2015), mangroves (Numbere, 2019), the Arctic (Vestergaard *et al.*, 2018) and oceans (Pirotta *et al.*, 2019).

The restoration of post-mining landscapes may also act as a potential pathway for the introduction of alien and invasive alien species. For example, several studies highlight the use of alien species in restoration activities (Mayonde *et al.*, 2015; Oliphant *et al.*, 2017). In South Africa, alien *Tamarix* (tamarisk) species, which have been used in the restoration of post-mining landscapes, have since hybridized with indigenous *Tamarix* species, posing a potential risk for future biological invasions by hybrids (Mayonde *et al.*, 2015; **section 3.3.5.1**). In the United States, the planting of the alien shrub *Elaeagnus umbellata* (autumn olive) has resulted in spread of the species beyond the sites of introduction, which hinders vegetation recovery (Oliphant *et al.*, 2017). Post-mining areas may also be considered as potentially suitable sites for the cultivation of biofuel feedstocks from known invasive alien species, which may spread beyond the area of introduction due to the inherent invasive traits of the species. While the outcomes of introducing known invasive alien species to improve soil conditions where native vegetation is unable to grow due to contamination is beneficial, introducing new species to areas where they were not before (Prabakaran *et al.*, 2019) may increase the risk of alien species spreading to new areas. A meta-analysis of small mammal recovery in passive and actively restored mining areas (Lawer *et al.*, 2019) found that the abundance of invasive alien species was significantly higher in actively restored areas compared to native species. Similarly, studies on the vegetation composition of four coal mines in the Yunnan Province, China, found that invasive alien species occur mainly in degraded areas where active mining or restoration activities are taking place (Hou *et al.*, 2019). However, invasive alien species occurrence can also be influenced by the type of mine and the material extracted (Hou *et al.*, 2019). In a review of the recovery of post-mining landscapes from North America, Europe and Australia, Macdonald *et al.* (2015) found that native species recovery was slowed by the establishment of invasive alien plants.

The evidence for mining as a driver of change in nature that facilitates biological invasions reported in this section stems mainly from terrestrial and marine realms and from Europe and the Americas. Most evidence exists for the introduction, establishment and spread of plants and trees, with little representation of other taxa apart from mammals.

3.3.3 Pollution

Pollution entails releasing new chemical or physical substances or increasing the level or concentration of already-existing substances into ecosystems. Although there are no consistent global assessments on the increase and impacts of pollution, it is believed that pollution has increased at rates similar to the total population growth (IPBES, 2019). Pollution can facilitate invasive alien species through increasing nutrient and resource levels available in ecosystems, such as is the case with eutrophication (**section 3.3.3.1**), through introducing new chemical substances in water or soil (**section 3.3.3.2**) and through dispersal of solids (**section 3.3.3.4**). Marine debris (notably, plastics) are treated separately (**section 3.3.3.3**) because they are a major emerging issue in the context of biological invasions. These pollution sources stem from major economic (**section 3.2.3**) and demographic (**section 3.2.2**) indirect drivers. **Section 3.3.3** thus describes evidence for links between specific pollutants and invasive alien species **(Figure 3.18)**, and makes reference to other indirect and direct drivers when relevant, whereas the demographic and economic background of these changes are described in **section 3.2**.

3.3.3.1 Eutrophication and nutrient deposition

Eutrophication refers to the increase of macronutrients, primarily nitrogen and/or phosphorus in the environment. Major sources are fertilizer use, runoff from animal husbandry and combustion by-products (Stevens, 2019). Common pathways for eutrophication are atmospheric deposition (a major source of oxidized nitrogen) and

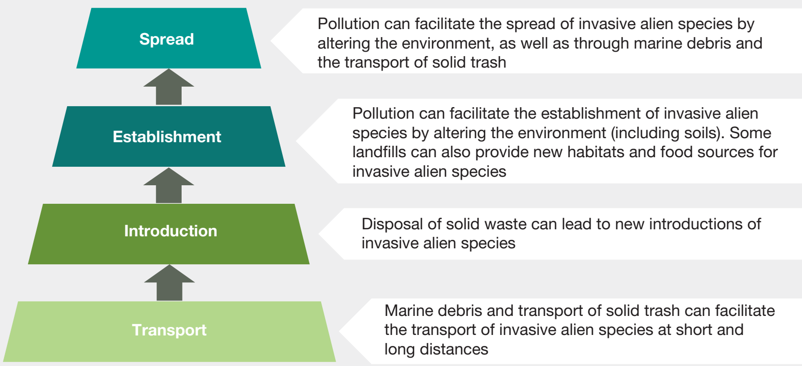


Figure 3 18 **Examples of the role of pollution as a driver of change in nature that facilitates invasive alien species across stages of the biological invasion process.**

Solids (marine debris, solid waste) can facilitate the transport and introduction of invasive alien species and provide habitat and surfaces where alien species can establish and spread. Nutrient and chemical pollution can change habitat quality, making sites more hospitable to invasive alien species.

run-off (nitrogen, phosphorous and other macronutrients, particularly affecting freshwater and coastal systems). The global use of fertilizers increased linearly during the second half of the twentieth century (IPBES, 2019), and for many regions a further increase in the balance of both nitrogen and phosphorus in the soil is expected in the following decades (FAO, 2015). Accordingly, during the last decade alone, there was a four to 20 fold increase in nitrogen flux in aquatic ecosystems (IPBES, 2019). Initial emissions are driven by economic (**section 3.2.3**) and demographic drivers (**section 3.2.2**), as described in the IPBES Global Assessment (IPBES, 2019). Pollution may interact with land- and sea-use change (**section 3.3.1**) and climate change (**section 3.3.4**) in driving the establishment and spread of alien species.

Invasive alien plant species often originate from relatively nitrogen-rich habitats (Dostál *et al.*, 2013), and are hence hypothesized to be more likely to establish and spread under increased nitrogen availability. In line with this, replicated experiments across hundreds of sites in Arctic, boreal, temperate, Mediterranean and tropical grasslands demonstrate that nitrogen addition generally increases the occurrence, abundance, and impact of invasive alien plants, a pattern that is especially pronounced towards warmer and wetter sites (Borer *et al.*, 2017; Seabloom *et al.*, 2013). A review from the United States reported that in temperate and Mediterranean temperate vegetation, increased abundance of invasive alien species is consistently documented as an impact when nitrogen deposition exceeds the critical load for that vegetation type (Pardo *et al.*, 2011). Nitrogen deposition and eutrophication have also been associated with increased abundance of alien tree and understory plant species in a wide range of other habitats, including tropical humid forests (Cusack *et al.*, 2016), temperate forests (Gilliam, 2006) and European lowland heaths (Fagúndez, 2013). Urban and other strongly human-impacted areas may be especially susceptible to invasive alien species facilitated by eutrophication (Ladd, 2016). Eutrophication may also interact with and feedback to other drivers in facilitating invasive alien species, for example, several reviews find that across Mediterranean-type ecosystems, nitrogen deposition favours alien grasses, which accumulate dead biomass in the dry season, increasing wildfire risk (Ochoa-Hueso *et al.*, 2011; Ochoa-Hueso & Manrique, 2010; Vasquez *et al.*, 2008; **section 3.3.1.5.2**).

In aquatic systems, a global study of invasive alien chironomids found that a high proportion of the reported cases were from eutrophic waters, including anthropogenic urban lakes and drainage channels and wastewater treatment plants (Linders *et al.*, 2020). Eutrophication also facilitates alien algae invasions in European lakes and streams (Wilk-Woźniak & Najberek, 2013) and aquatic plant invasions in China (Wu & Ding, 2019). A meta-analysis of drivers of change in freshwater systems revealed surprisingly few studies that explicitly consider alien species (Alahuhta *et al.*, 2019). A review of over 400 marine algal invasions found that most invasive alien species were encountered in eutrophicated waters, but also points out that several vectors and disturbances correlate with eutrophication, and that there is a general lack of experimental studies so it is difficult to establish causality (S. L. Williams & Smith, 2007). A well-studied biological invasion by the potentially toxic dinoflagellate *Prorocentrum minimum* in the Baltic Sea was empirically linked to eutrophication (Hajdu *et al.*, 2005). Eutrophication caused by aquaculture can be particularly conducive to macroalgal invasion in former seagrass beds (Boudouresque *et al.*, 2021; Gennaro & Piazzi, 2011). Extreme eutrophication in aquatic systems can lead to hypoxia. Upon recovery, empty niches may be filled with opportunistic invasive alien species, as shown for an invasive alien nematode which dominates areas of the recovering Ems estuary on the border between the Netherlands and Germany (Essink, 2003).

Studies of eutrophication as a driver affecting invasive alien species are most often focused on plants and algae as they are autotrophic and take macronutrients up directly from the environment. Such studies focus on the establishment and spread phase of the biological invasion process and most focus on alien species of vascular plants in Europe and North America (the geographic bias in these studies largely reflecting overall bias in the location of scientific studies). The available evidence suggests that the role of eutrophication in driving biological invasions is often variable, and both species- and system-specific. On one hand, alien species that respond positively to nitrogen availability in their native range also tend to respond positively to high nutrient availability in their invaded ranges (Borer *et al.*, 2017). On the other hand, in the absence of extrinsic nutrient addition, or in systems where nutrient addition *per se* does not lead to increased productivity or growth, such as for example in tropical forests, alien species can nevertheless benefit from nutrient addition (Cusack *et al.*, 2016). Marine studies are particularly focused on the spread of invasive alien species in Mediterranean seagrass ecosystems.[7] Authors found no studies directly linking eutrophication to terrestrial vertebrate invasions, despite the potential for a link between soil nitrogen and invasive alien herbivores *via* bottom-up processes.

3.3.3.2 Other contaminants in water and soil

Human modification of environments due to high pressure on direct exploitation of natural resources (**section 3.3.2**), land-use change (**section 3.3.1**) and urbanization (**section**

7. Data management report available at https://doi.org/10.5281/zenodo.5529309

3.2.2.4) has led to deposition of diverse contaminants in soil and water. Construction and maintenance of roads introduces metals (especially lead, but also aluminium, iron, cadmium, copper, manganese, titanium, nickel, zinc and boron), salts, ozone and nutrients into roadside environments (Trombulak & Frissell, 2000). This introduction creates an opportunity for alien species that are highly tolerant to contaminants to establish in areas where native species are struggling. For example the roadside *Melinis repens* (natal redtop) is a common naturalized species in Australia and high levels of trace metal were found in its tissues (C. Pratt & Lottermoser, 2007). Zhang *et al.* (2008) found that higher tolerance to lead stress enabled the alien *Sambucus canadensis* (American black elderberry) to outperform the native *Kummerowia striata* (Japanese lespedeza) and may have promoted its rapid establishment in lead contaminated soil. In Brazil, in a rocky neotropical savannah, Barbosa *et al.* (2010) found that paved roads, by reducing aluminium toxicity, favour alien species and helps them during the first stages of the biological invasion process. However, in some cases, soil contamination can also limit the fitness of invasive alien species and influence the dynamics between invasive alien and native species. De la Riva and Trumble (2016) investigated the effect of selenium on reproduction and competitive behaviour of the invasive alien *Linepithema humile* (Argentine ant) and found environmental toxins may not only pose problems for native ant species, but may also serve as a potential obstacle for establishment among alien species; *Linepithema humile* reproduced less when exposed to selenium.

Pollutants in aquatic systems, including metals contained within antifouling paints, can enhance the establishment success of invasive alien species (Piola & Johnston, 2008), particularly those that have a positive association with metal contamination such as the invasive alien hull-fouling bryozoan *Watersipora subtorquata* (McKenzie *et al.*, 2012). Additionally translocations of static maritime structures and movement of semi-submersible rigs continue apace in the Anthropocene and so act as largely overlooked and unregulated vectors of marine invasive alien species (Iacarella *et al.*, 2019; Wanless *et al.*, 2010). Also, water pollution caused by high alkalinity and nitrate concentration (**section 3.3.3.1**) is associated with the occurrence of aquatic invasive alien species that are among Europe's top 10 invasive alien species, such as *Dreissena polymorpha* (zebra mussel), *Procambarus clarkii* (red swamp crayfish) and *Salvelinus fontinalis* (brook trout) (Gallardo, 2014).

3.3.3.3 Marine debris

Marine debris is defined as "any persistent manufactured or processed solid material discarded, disposed of or abandoned in the marine and coastal environment" (Agamuthu *et al.*, 2019), thus dispersal of any alien species through marine debris is considered anthropogenic. The six main categories of marine debris are plastic, paper, metal, textile, glass and rubber (Agamuthu *et al.*, 2019). Plastic comprises 50 to 90 per cent of the total marine debris found globally (Eriksen *et al.*, 2014). A 2014 estimate of the amount of plastic pollution floating on the ocean revealed that there is a minimum of 5.25 trillion particles weighing 268,940 tons (Eriksen *et al.*, 2014). In the absence of further regulations, the amount of plastic entering aquatic ecosystems annually is expected to increase from 14 million tons per year in 2016 to 23-37 million tons per year by 2040 (United Nations Environment Programme, 2021). This burgeoning amount of plastic debris in the ocean has created unprecedented opportunities for the dispersal of marine organisms through rafting, representing a potential mechanism for biological invasions. Floating marine debris can disperse attached organisms significant distances depending on the ocean current speed and direction, and thus facilitates first introductions (*via* long-distance transport) to a new region, and secondary spread (short-distance transport) within an invaded region (Rech *et al.*, 2016). Floating plastic degrades much more slowly than natural rafting material and therefore is a potentially more potent vector for long-distance dispersal of invasive alien species (Agamuthu *et al.*, 2019).

Flotsam and jetsam (floating debris) usually start their floating journey in a "clean" state (i.e., free of fouling biota). Debris provides a new habitat for marine species adding new surfaces for colonization by organisms. Because debris usually spends a long time periods in the marine environment, debris often hosts an extensive and reproductively active fouling biota, before becoming part of marine floating litter (Kiessling *et al.*, 2015). For example, in Colombia, 86 per cent of marine debris is composed by wooden materials and plastic litter, which generate the optimal conditions for species to float away and colonize novel areas. Indeed, this study found that 62 per cent of the surveyed beaches were found to have marine fauna using floating plastic or wood as a substrate for potential rafting and dispersal (Gracia C. *et al.*, 2018). Organisms ranging from algae to reptiles (i.e., iguanas) have been observed to raft on floating objects, but the most common species include barnacles, polychaete worms, bryozoans, hydroids and molluscs. There is evidence for the transport of 270 species belonging to 85 taxa, including at least five invasive alien species on floating objects on the sea; however this phenomenon is likely still underestimated due to the limited number of studies and observations at the species level (Avio *et al.*, 2017). The highest numbers of rafting taxa on floating litter were found in the Pacific and North Atlantic, which might be explained by the overall high research effort undertaken in these regions (Kiessling *et al.*, 2015).

Marine plastic debris is largely attributed to fisheries and leisure or household gear (Gracia C. *et al.*, 2018). Off the

Asturian coast, Spain, rafting biota identified included species of goose barnacles, acorn barnacles, bivalves, gastropods, polychaetes and bryozoan, and hydrozoan colonies attached to stranded litter, many of which were alien species, such as *Magallana gigas* (Pacific oyster) and *Austrominius modestus* (Australian barnacle) (Rech *et al.*, 2018). Plastics, except for foam, sustained a more diverse attached community than non-plastic materials (Rech *et al.*, 2018). Another study carried out in New Zealand identified that the most common biofouling taxa traveling in marine debris were hydroids, bryozoans, algae and polychaetes (Campbell *et al.*, 2017). Off the Cantabrian Coast, alien species expansions could be reinforced by the presence of manufactured objects in the sea. *Austrominius modestus, Magallana gigas*, the potentially invasive alien *Amphibalanus Amphitrite* (striped barnacle) and other 14 species were found attached to plastic bottles and fishing gear, in particular on ropes (Miralles *et al.*, 2018). Off the west coast of Svalbard, a study that assessed the density of macro-plastic litter and the biota established on them found that the largest objects (fishing boxes, containers) were colonized by *Semibalanus* sp. (barnacles), *Lepas* sp. (goose barnacles), *Mytilus* sp. (blue shells), bryozoans and marine macro-algae.

Box 3 8 The spread of invasive alien species on Japanese tsunami marine debris.

On the 11 March 2011, an undersea megathrust earthquake struck Japan and created a tsunami on its East coast (specifically in the Tohoku coast of Northeast Honshu, Japan) that reached 38.38 m in height (Carlton *et al.*, 2017; Shimada, 2016). The tsunami produced abundant marine debris and caused the translocations of multiple taxa that were concentrated in the Pacific Northwest of the United States. At least 289 living Japanese coastal marine species have been found since 2012 on the coastlines of North America and Hawaii; the biota included macroinvertebrates, fish, microinvertebrates and protists (Carlton *et al.*, 2017). According to Miller *et al.* (2018), one of the most common species arriving on Japanese tsunami marine debris is *Mytilus galloprovincialis* (Mediterranean mussel). During the following years after the tsunami, various reports associated the appearance of new invasive alien species, not previously reported, with this event. The establishment of rafting species will depend on the number and frequency of reproductively viable individuals being transported on the marine debris coupled with the presence of suitable environments in the recipient range (Carlton *et al.*, 2017). The tsunami occurred early in the breeding season for many coastal species, which may have contributed to a successful settlement on Japanese tsunami marine debris (J. A. Miller *et al.*, 2018).

Figure 3 19 Marine debris caused by the 2011 tsunami in Japan.

The derelict was discovered off the coast of Seal Rock, Oregon, USA in April 2015 after having been missing from Japan since the tsunami on 11 March 2011. Photo credit: John W. Chapman – under license CC BY 4.0.

The rafting of groups of adult organisms favours their better biological dispersal compared to larval transport, and is regarded as the main reason for reappearance of the genus Mytilus on Svalbard (Weslawski & Kotwicki, 2018). In the western Mediterranean Sea, plastics were the major type of debris found because of its poor degradability; however, glass, cans, fishing nets and polyurethane containers were also found. Macro-benthos living on raft material comprised mainly molluscs, polychaetes and bryozoans, large fish were found commonly below large plastic bags, while following resources linked with the bags, these fish might move outside of their native range (Aliani & Molcard, 2003). Non-plastic objects, while less abundant and less ephemeral, can still help in spreading invasive alien species, as shown by an example of 10 alien mollusc species found on a single buoy (Ivkić *et al.*, 2019).

Marine debris can interact with other drivers in facilitating biological invasions. Notably, natural disasters can enhance the movement of invasive alien species traveling on marine debris (**section 3.4.1**). For several years following the Japanese tsunami in 2011, debris with living species from Japan has landed on coastlines from Midway Atoll to Hawaii Island and from south central Alaska to central California **(Box 3.8)**. Using the data from this event to model potential establishment, Simkanin *et al.*(2019) found that of 48 invertebrate and algal species on the Japanese tsunami marine debris, 27 per cent (13 species) had landed on Asturian coast locations with suitable environmental conditions for establishment and survival, and a further 43 per cent (21 species) had environmental requirements met in other areas where tsunami debris likely landed (but had not been documented).

3.3.3.4 Dispersal of solid waste

In 2016, humans generated over 2 billion tons of municipal solid waste, and by 2050 this number is predicted to increase to 3.4 billion (Kaza *et al.*, 2018). Solid waste can both transport and sustain a high variety of alien organisms, thus contributing to the spread of invasive alien species. A global review reported the establishment of 215 alien plant species in waste disposal sites (Plaza *et al.*, 2018). In Pakistan, industrial waste increased the recruitment of the invasive alien tropical trees *Prosopis juliflora* (mesquite) and *Leucaena leucocephala* (leucaena) (Uzair *et al.*, 2009). In central Brazil, the dispersal of the invasive alien grass *Arundo donax* (giant reed) seems to be assisted by the disposal of construction waste (Simões *et al.*, 2014). Disposal of garden waste may facilitate the spread of ornamental alien plant species, as examples, in Spain the cactus *Opuntia engelmannii* subsp. *lindheimeri* (Lindheimer pricklypear; Elorza *et al.*, 2004), in Argentina, the fast-growing liana *Podranea ricasoliana* (pink trumpet vine; Hurrell *et al.*, 2012) and the rhizomatous fern *Pteris parkeri* (Cretan brake; Guerrero, 2017). Dumping garden waste in close proximity to watercourses contributed to the spread of *Reynoutria sachalinensis* (giant knotweed) and *Reynoutria japonica* (Japanese knotweed) in riparian habitats in the Czech Republic (Pyšek & Prach, 1996). Irresponsible disposal of fragments of alien aquarium macrophytes and macroalgae may promote their introduction and spread in nature (Cohen *et al.*, 2007; Odom *et al.*, 2014; Vranken *et al.*, 2018). Waste disposal sites are a source of propagules of alien plants that can spread into natural habitats. In central Brazil, savannah adjacent to landfills has ten times more alien species than nearby savannah not adjacent to landfills (Santana & Encinas, 2008). Urban mixed deciduous forest sites in Switzerland close to illegal garden waste dumping areas exhibit over 30 times more alien species than nearby control areas (Rusterholz *et al.*, 2012). In addition, landfill areas used for compost production may contain many alien plants (Vaverková *et al.*, 2020), so that the distribution and use of this compost, for example in agriculture, could promote biological invasions (Pietsch, 2005).

Waste disposal sites are often used as a food source by alien vertebrates found close to urban areas (**section 3.2.2.4**), such as *Rattus norvegicus* (brown rat), *Felis catus* (cat) and *Sus scrofa* (feral pig) (Plaza & Lambertucci, 2017). Food waste has been found to be an important item in the diet of feral cats in Mexico (Ortiz-Alcaraz *et al.*, 2017) and Australia (Hutchings, 2003), and a rubbish tip in Australia supported a high density of feral cats (Denny *et al.*, 2002). Among alien birds, food waste consumption has contributed to the establishment and spread of *Threskiornis aethiopicus* (sacred ibis) in the United States (Calle & Gawlik, 2011) and Western Europe (Clergeau & Yésou, 2006), as well as for *Passer domesticus* (house sparrow) in urban sites in Kenya (Imboma, 2014). In eastern Madagascar, the abundance of the invasive alien *Duttaphrynus melanostictus* (Asian common toad) is positively related to the presence of rubbish dumps (Licata *et al.*, 2019). Disposal of green waste containing small alien vertebrates may also contribute to their spread, as was possibly the case during the rapid expansion of *Leiocephalus carinatus armouri* (northern curly-tailed lizard) in Florida (H. T. Smith & Engeman, 2003). In South Central United States, landfills facilitate the establishment and spread of *Paratrechina fulva* (tawny crazy ant; ISAC, 2016). In South America, waste disposal sites provide food and hiding sites for *Lissachatina fulica* (giant African land snail; Gregoric *et al.*, 2013; Kaique & Nara, 2017; Thiengo *et al.*, 2007). Alien species account for 30 per cent of the richness and abundance of macro-snails in landfills in the United Kingdom (Rahman *et al.*, 2016). The accumulation of water in solid waste disposed in urban areas favours the proliferation of alien mosquitos of the genus *Aedes*, which are vectors of several diseases that affect humans (e.g., *Aedes aegypti* (yellow fever mosquito); Baldacchino *et al.*, 2015).

In summary, the disposal of solid waste has contributed to the introduction, establishment and spread of a wide variety of alien plant and animal species in terrestrial and aquatic habitats across continents. Most of the studies took place in Europe and North America. There is a lack of studies in the East Asia and Pacific regions, where the highest amount of solid wastes are produced (Kaza *et al.*, 2018).

3.3.4 Climate change

Anthropogenic climate change has emerged as a dominant threat to Earth's biodiversity and ecosystems over the last few decades, altering species' ranges and abundances, reshuffling biological communities, restructuring food webs, and altering ecosystem functions (IPBES, 2019; IPCC, 2022). Alterations in global temperature and precipitation regimes are predicted to facilitate biological invasions by increasing the likelihood of introduction and establishment of invasive alien species in many areas, thus increasing the potential invaded range of invasive alien species (Hellmann *et al.*, 2008; IPBES, 2019; IPCC, 2022; Walther *et al.*, 2009). Climate change may further facilitate biological invasions by increasing rates of reproduction and survival in sites where invasive alien species are already present, hence facilitating their establishment and further spread (Chown *et al.*, 2012; Fløjgaard *et al.*, 2009; Loomans *et al.*, 2013). The range or population growth rates of some alien species may currently be limited by climatic variables which may become more favourable in the future (e.g., low temperature, low precipitation in regions where these climate factors show increasing trends; Bradley *et al.*, 2010; Ibáñez *et al.*, 2009; O'Donnell *et al.*, 2012). Some studies based on bioclimatic models predict that more frequent extreme events may have potential to trigger or alter the trajectory of biological invasions (Hulme, 2017; Pyšek *et al.*, 2020). While models and projections point to potentially strong impacts of climate change on biological invasions (**section 3.6.3**, **Box 3.14**), empirical data that unambiguously attribute shifts in alien species' distributions and abundances to climate change are rare.

Climate change entails shifts in both mean conditions and the frequency and magnitude of climatic extremes, all of which can have consequences for biological invasions. This section synthesizes knowledge about how invasive alien species are affected by changes in temperatures (**section 3.3.4.1**), precipitation regimes (**section 3.3.4.2**), extreme events (**section 3.3.4.3**), CO_2 concentrations (**section 3.3.4.4**), fire frequencies and magnitudes (**section 3.3.4.5**), sea level rise (**section 3.3.4.6**), and, assisted colonization is an example of a climate mitigation strategy with high relevance for invasive alien species **(Box 3.9)**. Climate change results from major economic (**section 3.2.3**) and demographic (**section 3.2.2**) indirect drivers over long timescales. **Section 3.3.4** describes evidence for links between specific climatic changes and invasive alien species **(Figure 3.20)**, and makes reference to other indirect and direct drivers when relevant. The demographic and economic background or these changes are described in **section 3.2**.

3.3.4.1 Temperature change

Global mean surface temperature is projected to rise between 1.4°C and 4.4°C by the end of the twenty-first

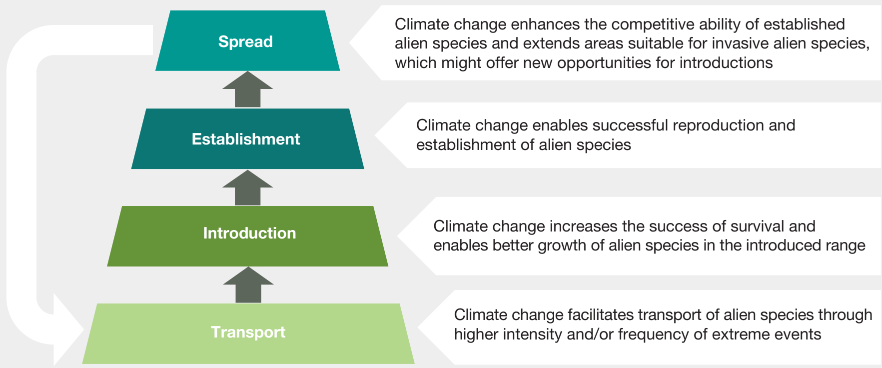


Figure 3 20 **Examples of the role of climate change as a driver of change facilitating invasive alien species across stages of the biological invasion process.**

Extreme events may facilitate transport, changes in climatic conditions may enhance survival, reproduction, and competitive ability, which in turn increases introduction establishment and spread, of alien species. Climate change may extend the geographic ranges potentially suitable for invasive species, providing potential feedback from spread (within the invaded range) to transport (to new areas beyond the current invaded range). Adapted from Walther *et al.* (2009).

Box 3 9 **Assisted colonization.**

Species translocations for conservation purposes have been conducted for decades, but the vast majority are reintroductions or population enhancements of species within their historical range, whereas assisted colonization (variously termed "assisted colonization", "assisted migration" and "managed relocation"; Hoegh-Guldberg *et al.*, 2008; J. M. Mueller & Hellmann, 2008; Richardson *et al.*, 2009) is concerned with moving species into areas beyond the range in which they have a recent evolutionary history. Assisted colonization could become a significant driver facilitating biological invasions in the future as climate change adaptation and ecosystem restoration strategies increasingly argue for species translocation (D. M. Hansen, 2015; Lunt *et al.*, 2013). Thus far, assisted colonizations of animals have typically involved relatively short-distance translocations, most often to islands (e.g., Freifeld *et al.*, 2016; Griffiths *et al.*, 2010; Scoleri *et al.*, 2020). Since the mid-2000s there have been an increasing number of proposals to intentionally introduce plants and animals to favourable habitats beyond their historical ranges, with the goal of protecting such species against climate change and other environmental stressors (Seddon, 2010).

It has been proposed that decisions regarding assisted colonization schemes can be guided safely by an assessment of the costs and benefits of translocation (Hoegh-Guldberg *et al.*, 2008), including the potential ecological or economic impacts of biological invasions. Others have argued that the ability of ecologists to forecast ecological costs is weak (Ricciardi & Simberloff, 2009). Some researchers suggest that the risks of ecological disruption can be reduced by moving species within the same continent (J. M. Mueller & Hellmann, 2008), especially where closely related species exist. In such situations the translocated species is less likely to encounter communities that lack eco-evolutionary experience with functionally similar taxa and thus the species' abundance and impact are more likely to be constrained through species interactions; however, this rationale ignores risks of hybridization, competitive displacement and disease transmission (Arcella *et al.*, 2014; Morales *et al.*, 2013; Simler *et al.*, 2019). Given the global influence of climate change as a stressor, the issue of assisted colonization is relevant to biotas in all regions and terrestrial, freshwater and coastal marine realms.

century (2081–2100) relative to 1986–2005, depending on how greenhouse gas emissions develop (Arias *et al.*, 2021; IPCC, 2014, 2021). Warming seems to be strongest at high northern latitudes and with variable rates in mountainous biomes in comparison to lowlands (Loarie *et al.*, 2009; Mountain Research Initiative EDW Working Group, 2015; C. Nolan *et al.*, 2018; Q. Wang *et al.*, 2016). The warming is associated with other changes in ecosystems such as contraction of snow cover and permafrost areas (Luláková *et al.*, 2019) and increased risk of heat and precipitation extremes (IPCC, 2007, 2021) affecting the productivity and water-use efficiency and spatial shifts of habitats (Svenning & Sandel, 2013).

The general expectation is that with increasing temperatures, some established alien species will be able to expand their ranges polewards and to high elevations and thus expand their introduced ranges without additional human assistance. Warming is a major component in forecasts of the responses of 100 of the world's worst invasive alien species to climate change, according to the International Union for Conservation of Nature (IUCN), who project significant range shifts, and hence further spread of invasive alien species within and beyond their current invaded ranges (Bellard *et al.*, 2013). For example, outbreaks of bluetongue virus, a disease of ruminants transmitted by *Culicoides* species (biting midges), occurred for the first time in northern Europe in 2006 as a result of warmer temperatures. In the future, these northern regions will become increasingly suitable for this midge vector, which could spread unaided on prevailing winds (A. E. Jones *et al.*, 2019). Increased temperatures may benefit the establishment of some alien species regularly intercepted at the border by quarantine officers as contaminants of goods (particularly agricultural and horticultural produce) or stowaways on transport vectors (such as in or on boats). Since the 1970s, the establishment in the United Kingdom of alien invertebrate plant pests intercepted at ports of entry or for which outbreaks have been reported is positively correlated with average winter temperatures, but no such relationship was found for plant pathogens (Hulme, 2017). However, increases in winter temperature was found to facilitate the spread of plant pathogens in North America (Kliejunas, 2011).

Climate change may increase the probability of establishment and spread of alien species that are currently present in a particular region in anthropogenic environments such as buildings, glasshouses, and gardens but are limited by climate from surviving in nature. For example, in the United Kingdom warmer winter temperatures are expected to increase the probability that *Liriomyza huidobrensis* (serpentine leafminer) and the soil-borne *Athelia rolfsii* (sclerotium rot), currently found in glasshouses, will be able to overwinter outside and consequently establish (Baker *et al.*, 1996; Hardwick *et al.*, 1996). Similarly, casual annual C4 weeds (e.g., *Setaria viridis* (green foxtail), *Digitaria sanguinalis* (large crabgrass)) that do not tolerate frost and thus do not currently survive the winter in the United Kingdom may become problematic in arable agriculture in a warmer future when this constraint is lifted, especially as they are well-adapted to high temperatures that some British native plants may not tolerate as well (Froud-Williams, 1996). For insects in temperate regions, a major effect of climate warming is enhanced individual growth and development and consequent increased winter survival, allowing range expansion to more northerly latitudes (Bale *et al.*, 2002). Thus several invasive alien insect species, many of which are crop pests and diseases, may expand their ranges northward and upward under climate change (Lehmann *et al.*, 2020). In aquatic systems, substantial non-breeding populations of the *Trachemys scripta* (pond slider) have persisted for some time in regions where climate change could soon facilitate reproduction and subsequent establishment and spread (Rödder *et al.*, 2009). Similarly, warming of North American lakes is likely to increase thermal suitability for species of fishes currently with a more southerly distribution, including many alien species, that could potentially expand their distribution poleward into alien regions, potentially as far as the Arctic (Ricciardi *et al.*, 2020).

Several empirical studies support and confirm some of these projections. Higher temperatures, extended summer seasons, and increasing available thermal budget for growth are recognized as potential explanations for ongoing polewards shifts in species' distributions (S. C. Mason *et al.*, 2015; Parmesan & Yohe, 2003). There is evidence that alien species may be especially well-suited to exploit opportunities for range expansions offered by warming. For example, over the past two decades, alien plant species in the European Alps have colonized higher altitudes approximately twice as rapidly as native species (Dainese *et al.*, 2017). As another example, the majority of alien species in the Mediterranean originate from the Red Sea (i.e., Lessepsian migrants; about 67 per cent of all alien species; **section 3.3.1.3**, **Box 3.7**), with a small proportion (about 7 per cent) from other tropical areas. These alien species have long been confined to the easternmost Levantine shores, and the warming of the Mediterranean is now facilitating their further spread (Lejeusne *et al.*, 2010). Temperature has been found to limit key performance parameters in alien species across taxonomic groups and regions, including fecundity in mammals (D. J. Bell & Webb, 1991), fish (Fobert *et al.*, 2011) and birds (Shwartz *et al.*, 2009); growth in marine algae (Hales & Fletcher, 1989) and fish (Kornis *et al.*, 2012); survival in amphipods (Ashton *et al.*, 2007; Cowling *et al.*, 2003) and mosquitoes (Roiz *et al.*, 2011) and growth, survival and fecundity in plants (Willis & Hulme, 2002). However, temperature sensitivity in such performance parameters does not automatically translate into increased performance in a warming climate. For example, in the United Kingdom, alien plants have a faster phenological response to warming than co-occurring native species, yet this has not translated into a faster spread (Hulme, 2011b).

As climate change progresses, some regions, biomes and taxonomic groups will be subjected to climates not previously encountered, and invasive alien species are projected to either decrease or increase (Bellard *et al.*, 2013b; **Chapter 2**, **section 2.6**). Bellard *et al.* (2013) project future hotspots of invasive alien species to be in biomes at higher latitudes where future climate change is projected to be less extreme (e.g., temperate mixed forests and woodlands) whereas biomes expected to shift into extreme climatic zones (e.g., tropical forest) may experience a decrease in number of invasive alien species. The ranges of invasive alien terrestrial and aquatic invertebrates, aquatic plants and microorganisms are projected to increase, whereas the ranges of invasive alien amphibians, birds and fungi could experience range contractions under future climate projections (Bellard *et al.*, 2013b; **Chapter 2**, **section 2.6**).

3.3.4.2 Precipitation change

Climate change has caused an increase in global average precipitation since the mid-twentieth century, which has been accelerating since the 1980s, but with great regional and temporal variability, so that precipitation is increasing in some regions, decreasing in others, with interannual variability and seasonality also changing (IPCC, 2021). Few studies explicitly link biological invasions to precipitation change, and effects of precipitation change may relate both to water *per se* and to consequences for disturbance regimes or dispersal. Precipitation extremes cause disturbances which can create open sites suitable for colonization, especially in and along streams where precipitation extremes may also be associated with increased propagule pressure, leading to increased risk of biological invasions (Pyšek, Bacher, *et al.*, 2010). For example, drought and changes in flow regimes of rivers and streams (which are of relevance for precipitation change) can facilitate the spread of invasive alien plant species along streams in Europe, both directly and through negatively affecting the native plant community (Catford *et al.*, 2011, 2014). As another example, invasive alien European *Bromus* spp. grasses in North America can exploit available soil moisture more efficiently and thus recover more rapidly than native vegetation after drought enabling them to invade areas formerly dominated by native woody species following periods of drought (Ricciardi *et al.*, 2020). Precipitation changes may interact with temperature changes in affecting future ranges of invasive alien species. For example, the potential invaded range of *Bactrocera dorsalis* (Oriental fruit fly), a major pest throughout South East Asia that has invaded (and been eradicated from) a number of Pacific Islands and mainland areas in North America and elsewhere is projected to extend further polewards as cold stress boundaries recede, but also contract in areas where precipitation decreases substantially (Stephens *et al.*, 2007). In North America, concurrent changes in precipitation and temperature are projected to extend the potential invaded range for many invasive alien species of forest ecosystems (Dukes *et al.*, 2009). In particular, forest fungal pathogens in

Europe (123 taxa, of which 42 per cent are considered to be alien species) and North America (18 taxa) are sensitive to both low temperatures and drought, and are generally expected to extend their invaded ranges with increasing temperature and precipitation (Dukes *et al.*, 2009; Santini *et al.*, 2013). Precipitation change may also affect the distribution of invasive alien insects. *Solenopsis invicta* (red imported fire ant) was introduced to the United States from sub-Amazonian South America (native range) in the 1930s or 1940s, and has since expanded throughout North America and to Australia and New Zealand along with a number of tropical islands. The potential invaded range of the red imported fire ant is limited by both low temperature and low precipitation, and future projections entail both expansions and contractions, the latter largely in areas where precipitation is projected to decrease (Morrison *et al.*, 2004).

3.3.4.3 Climate extremes

Anthropogenic climate change is causing increasing frequency and/or intensity of climate extremes, including temperature extremes, heavy precipitation and pluvial floods, river floods, droughts, storms (including tropical cyclones), as well as compound events (IPCC, 2021). High-temperature extremes (including heatwaves) have become more frequent and more intense across most land regions since the 1950s, and marine heatwaves have approximately doubled in frequency since the 1980s (IPCC, 2021). The frequency and intensity of heavy precipitation events have increased since the 1950s over most land area, and agricultural and ecological droughts have increased in some regions due to increased land evapotranspiration (IPCC, 2021). Climate extremes can cause dramatic ecosystem destabilization and an abrupt shift towards an alternative ecosystem state (Jentsch *et al.*, 2007), which may affect all stages of the biological invasion process (i.e., transport, introduction, establishment and spread; **Chapter 1**, **section 1.4**) (Hulme, 2017). However, global and quantitative assessments on the response of invasive alien species to extreme climatic events seem to be limited even for generally better-studied taxonomic groups such as plants (Orsenigo *et al.*, 2014) and insects (Bale *et al.*, 2002).

There is evidence that climate extremes (e.g., heavy winds, hurricanes, storms and floods) enhance long-distance transport and spread of invasive alien plants, vertebrates, invertebrates and invasive alien species that are agricultural pests and pathogens (Aylor, 2003; J. K. M. Brown & Hovmøller, 2002; Diez *et al.*, 2012; Hellmann *et al.*, 2008; Nagarajan & Singh, 1990). In terrestrial ecosystems, extreme hurricanes in Northern and Central America resulted in the long-distance spread of invasive alien weeds (Masters & Norgrove, 2010), alien vertebrates (e.g., *Iguana iguana* (iguana) and *Osteopilus septentrionalis* (Cuban treefrog); van den Burg *et al.*, 2019) and diseases (*Xanthomonas axonopodis* (gummosis: grasses); Masters & Norgrove, 2010). The frequency of hurricanes positively relates with the large-scale pattern of spread of alien *Phragmites australis* (common reed) in the United States (Bhattarai & Cronin, 2014).

In freshwater and marine biomes, extreme hydrological events (sometimes caused by strong winds) such as storms and floods may facilitate the transport, spread and establishment of invasive alien aquatic organisms (Anufriieva & Shadrin, 2018). Severe floods may allow fishes to escape from farm ponds and culture cages into natural water bodies (Canonico *et al.*, 2005). The Foe Indigenous People around Lake Kutubu in the Southern Highlands Province of Papua New Guinea have also observed the role of climate extremes in facilitating biological invasions. The shift from artisanal small-scale fishing to fish farming introduced alien fish (e.g., *Cyprinus carpio* (common carp)) and plants (*Pontederia crassipes* (water hyacinth)) to fish farms, which then escaped into Lake Kutubu during heavy rains of 2010-2012 (P. T. Smith *et al.*, 2016).

In polar ecosystems, genomic analyses revealed that *Durvillaea antarctica* (cochayuyo) has recently travelled more than 20,000 km by storm-forced surface waves (or oceanic storm waves) and reached Antarctica from mid-latitude source populations (C. I. Fraser *et al.*, 2018). In subarctic regions, extreme heatwaves cause hypoxia and high water temperatures, which seem to lead to widespread mortality of native freshwater fishes and facilitate the invasion of cool and warm water alien species (Rolls *et al.*, 2017).

Increased incidence and severity of heavy winds may also facilitate increased seasonal northward spread of plant pests and pathogens (Aylor, 2003; J. K. M. Brown & Hovmøller, 2002; Hopkinson, 1999; Olfert *et al.*, 2016, 2017), resulting in biological invasions beyond the current northern range limit of these species. For example, cereal rusts (Pucciniales) typically overwinter on cereals and grasses in the southern United States and northern Mexico, and the spores are blown northward in the spring or early summer by wind currents, affecting winter and spring cereal crops (Eversmeyer & Kramer, 2000; Xi *et al.*, 2015). Increased incidence and severity of heavy winds under climate change may enhance transport of rust species into the United States and Canada, thus facilitating biological invasions (Eversmeyer & Kramer, 2000; Xi *et al.*, 2015).

Extreme climatic events that cause catastrophic and widespread damage to ecosystems often increase the availability of resources such as water, nutrients, space and prey for alien species (Diez *et al.*, 2012; Hellmann *et al.*, 2008). In Australian rainforests, severe cyclones cause catastrophic disturbance by opening canopy gaps, thereby facilitating the rapid recruitment and spread of alien woody-vines (e.g., *Thunbergia* spp., *Mikania micrantha* (bitter vine) and *Turbina corymbosa* (Christmas vine); Camarero, 2019). Hurricane Sandy in the United States caused catastrophic coastal dune erosion and thereafter an alien *Carex kobomugi* (Asian sand sedge) established (Charbonneau *et al.*, 2017). Also, heavy drought can cause fire activity (e.g., 2019-2020 mega-fires in Australia and 2019 California wildfires, **Chapter 1**, **Box 1.4**), resulting in enhancement of the spread of invasive alien trees from plantation forests (**section 3.3.4.5**).

Extreme climatic events may also often stress and cause catastrophic mortality of resident native species, resulting in decreasing biotic resistance of native communities to the establishment and subsequent spread of invasive alien species (Diez *et al.*, 2012; Hellmann *et al.*, 2008; **section 3.3.5**). In semi-arid shrublands of Chile, a study based on 130 years of precipitation data showed that extreme drought, associated with El Niño effects, led to increased alien plant cover at the expense of native plants (Jiménez *et al.*, 2011). Similarly, using a mesocosm experiment across a precipitation and continental gradient between Belgium and Israel, Jentsch *et al.* (2007) found that drier ecosystems showed decreased biomass production after extreme droughts, facilitating invasive alien species establishment. These climatic extreme events also affected the resilience of marshes and riparian ecosystems. In Mexico, the vegetation of San Jose del Cabo (estuary) is resilient to hurricanes, but the vegetation cover loss due to the increased runoff caused by stronger hurricanes generated clearings that favoured the establishment of invasive alien species such as *Arundo donax* (giant reed) and *Tamarix* sp. (tamarisk) (Shiba-Reyes *et al.*, 2021).

Extreme climatic events can also act as a driver affecting the decline of invasive alien species. For example, a heavy drought in North America between 1987 and 1988 has led to the declines of 10 alien insect herbivore species in the following few years (Ward & Masters, 2007). An extreme cold spell in southern Florida led to declines in the abundance of an alien species, *Centris nitida* (oil-collecting bee), previously introduced from Mexico and Central America (Downing *et al.*, 2016).

3.3.4.4 Carbon dioxide enrichment in air, water

The concentration of atmospheric CO_2 in 2019 was 45 per cent higher (410 ppm) than in 1750; and in part excess CO_2 released from anthropogenic sources has been taken up by the oceans, ultimately leading to decreasing pH levels (IPCC, 2021). Responses to increasing atmospheric CO_2 differ between species within terrestrial and aquatic environments.

For terrestrial plants, higher levels of CO_2 cause an increase in water use efficiency and fertilization effects that can enable greater biomass production leading to an advantage of C4 rather than C3 plants (generally benefiting native relative to alien species; Nowak *et al.*, 2004). Nevertheless, winners and losers depend on availability of nutrients and some fast-growing C3 species (such as annual grasses) may respond more strongly than slow-growing C3 herbs or C4 plants (Poorter & Navas, 2003). In arid and semiarid ecosystems invasive alien annual grasses have a competitive advantage under elevated CO_2 (Chambers *et al.*, 2014; S. D. Smith *et al.*, 2000), whereas in savannahs, native grasses may be replaced by woody alien species (Bond & Midgley, 2000; Gritti *et al.*, 2006). These performance effects can translate to increased spread of invasive alien plant species and increased CO_2 concentrations. For example, invasive alien *Phragmites* spp. (reed) benefit from higher CO_2 concentrations and as a result increased dispersal and productivity allowing these species to compensate for transpiration water loss in the coastal marshes of North America (Eller *et al.*, 2014). Similar patterns of increased performance at higher than ambient CO_2 concentrations have been found for other invasive alien plants including *Prunus laurocerasus* (cherry laurel; Hattenschwiler & Körner, 2003) and *Pueraria montana* var. *lobata* (kudzu; Forseth & Innis, 2004). Terrestrial animal responses to the rise in CO_2 will likely be indirect, based on the responses of plants, and thus are likely to be most evident for herbivorous invertebrates but will be dependent on the specific host plant, making generalizations difficult (Dukes, 2000).

One-third of the anthropogenic CO_2 has been absorbed by the oceans (J. Johnson *et al.*, 2016; Sanford *et al.*, 2014). Together with warming and altered ocean circulation, which reduce subsurface oxygen concentrations, the rising atmospheric CO_2 leads to ocean acidification (Doney *et al.*, 2012). The impacts of acidification are more pronounced in extreme regions such as in polar regions (Fabry *et al.*, 2009) and for coral reefs where calcareous corals and algae are replaced by noncalcareous algae (Hall-Spencer *et al.*, 2008). In these regions, invasive alien species that are tolerant of high CO_2 concentrations increase in abundance, as documented for macroalgal biological invasions in the northeast Atlantic (Brodie *et al.*, 2014). In the Mediterranean Sea, invasive alien genera (e.g., *Sargassum, Caulerpa* and *Asparagopsis*) spread to sites where native coralline algae are disappearing due to acidified waters (Hall-Spencer *et al.*, 2010).

3.3.4.5 Fire regime changes

In addition to direct human-induced changes to fire regimes (**section 3.3.1.5.2**; **Chapter 1**, **Box 1.4**), weather conditions that favour fire occurrence (i.e., hot, dry and windy events) have become more common in some regions due to climate change, a trend that is expected to occur in even more regions in the future (IPCC, 2021). Climate change is expected to lead to more extreme and frequent fires globally (Hoegh-Guldberg *et al.*, 2018), and there is evidence that climate change during the last decades has already increased fire activity, for example in western United States (Abatzoglou & Williams, 2016; S. E. Mueller *et al.*, 2020). Likewise, recent increases in fire frequency and severity in eastern Australia, including the unprecedented estimated area of over 10 million hectares burnt during the 2019-2020 season (Boer *et al.*, 2020; R. H. Nolan *et al.*, 2020), are consistent with predicted changes in the fire regime under climate change (Clarke & Evans, 2019; Lewis *et al.*, 2019).

Fire may facilitate establishment and spread of invasive alien plants that exhibit highly effective post-fire regeneration, and presence of these species may in turn lead to changes in fuel properties that ultimately increase fire activity, thus promoting positive feedback mechanisms to the detriment of native species (Aslan & Dickson, 2020; Brooks *et al.*, 2004; Gaertner *et al.*, 2014; Rodewald & Arcese, 2016; Serbesoff-King, 2003; **Chapter 1**, **Box 1.4**; **Chapter 4**, **Box 4.5**). Accordingly, by leading to longer fire seasons, shorter fire return intervals and/or higher fire intensity than were previously encountered, climate change may favour the establishment and spread of fire-adapted invasive alien species (Abatzoglou & Kolden, 2011).

The effect of climate change on fire regimes will likely be intensified in the future and drive the spread of *Bromus tectorum* (downy brome) in deserts and Mediterranean ecosystems in the western United States (Abatzoglou & Kolden, 2011; Balch *et al.*, 2013). Higher fire activity under climate change may also drive the spread of the African grass *Cenchrus cilliaris* (buffel grass) in the central rangelands and eastern woodlands of Australia (D. W. Butler & Fairfax, 2003; G. Miller *et al.*, 2010). The mechanism for the spread of invasive alien grasses under climate change both in the United States and Australia is an intensification of fire-invasive positive feedback loops promoted by invasive alien species in these ecosystems (i.e., grass-fire cycle), where increased production of biomass by invasive alien grasses leads to increased fire frequency, continuity and/or intensity and hence favours their spread (Balch *et al.*, 2013; D. W. Butler & Fairfax, 2003; Gaertner *et al.*, 2014; G. Miller *et al.*, 2010). In addition, fire-induced air currents associated with the recent extreme fires in Australia seem to have driven the introduction of invasive alien species to New Zealand, such as the pathogenic fungi *Austropuccinia psidii* (myrtle rust; Australian Government, 2021), and could possibly also favour the arrival of the *Agrotis infusa* (bogong moth) in the country (Warrant *et al.*, 2016).

There is evidence that increased fire activity under climate change may also directly drive the spread of invasive alien woody species. In Patagonia, a warmer and drier climate is implicated in the spread of alien pines and shrubs whose persistence is promoted by fire (Cavallero & Raffaele, 2010; K. T. Davis *et al.*, 2019; Raffaele *et al.*, 2016). In European and southern African Mediterranean ecosystems, changes in the fire regime under a warmer and drier climate change are expected to favour the spread of invasive alien tree species from the genus *Acacia* (e.g., *Acacia longifolia* (golden wattle); Souza-Alonso *et al.*, 2017).

There is very limited information on how changes in fire regimes under climate change may facilitate the spread of invasive alien animals. In freshwater ecosystems in the western United States, increased fire activity due to climate change may favour alien fishes, especially in degraded and fragmented landscapes (Dunham *et al.*, 2003). In these ecosystems, larger and more frequent fires under climate change tend to increase water temperature and decrease stream stability and connectivity, thus driving the spread of generalist alien fishes to the detriment of native Salmonidae fishes (Isaak *et al.*, 2010; Luce *et al.*, 2012), although the effect of fire as a driver affecting invasive alien species in this region may be species-specific and less significant in comparison to other anthropogenic disturbances (Sestrich *et al.*, 2011).

3.3.4.6 Sea level rise

Global mean sea level increased 0.20 m from 1901 to 2018, with an annual increase of 3.7 mm per year from 2006 to 2018 (IPCC, 2021). Sea level rise is caused by climatic factors affecting the thermal expansion of water and the melting of glaciers, permafrost and polar ice sheets (Hoegh-Guldberg & Bruno, 2010; Oppenheimer *et al.*, 2019; Rignot *et al.*, 2018). Rising sea level will likely lead to increased impacts from extreme weather events and storm surges, increased coastal flooding, higher high tides and increased saltwater intrusion into freshwater systems, altering environmental conditions along coastal zones (Nicholls *et al.*, 2014; Woodruff *et al.*, 2013). Few studies have assessed the direct effect of sea level rise as a driver in the context of biological invasions. However, it is likely that marine invasive alien species able to disperse by ocean currents (e.g., *Mytilus galloprovincialis* (Mediterranean mussel)) may be introduced to new areas due to increased inundation of coastal areas (McQuaid & Phillips, 2000). In Hawaii, the combination of sea level rise and high tide events resulted in habitat creation, facilitating the spread of invasive alien fish (e.g., tilapias) from fishponds to nearby anchialine pools (Marrack, 2016).

Sea level rise, *via* the effect of saltwater intrusion into freshwater ecosystems and increased water salinity, may also shift selection pressures and facilitate the establishment of invasive alien species. Evidence from coastal areas in the United States (K. Williams *et al.*, 1999), Australia (Traill *et al.*, 2011) and China (W. Wang *et al.*, 2015) show that sea level rise may alter soil chemistry and native vegetation patterns in coastal wetlands or native forests, selecting for species with a higher tolerance to saline habitats and where present, allow invasive alien species to dominate. Increased tolerance of the alien haplotype of *Phragmites australis* (common reed) has allowed it to spread through native salt marshes in the Atlantic and Gulf Coastal areas (Bhattarai & Cronin, 2014; Vasquez *et al.*, 2005). Similarly, *Osteopilus septentrionalis* (Cuban tree frog), an invasive alien species in the United States, is tolerant to increased salinity which can facilitate its spread and establishment in coastal environments (M. E. Brown & Walls, 2013). Verbrugge et al (2012) found that salinity tolerance of *Corbicula fluminalis* (Asian clam) and *Potamopyrgus antipodarum* (New Zealand mudsnail) was higher than for native species occurring in the River Rhine. However, models of changes in salinity due to rising sea levels in the freshwater ecosystem of the Everglades indicate a decrease in alien fish species biomass (Romañach *et al.*, 2019) compared to native species.

In coastal systems, the effect of rising sea levels on soil moisture in coastal dune systems can disrupt sediment transfer impacting dune formation processes and vegetation patterns. For example, in New Zealand, increased soil moisture disrupts the formation of dunes (Thomas *et al.*, 2018) and allows for their colonization by plants, including the invasive alien grass *Calamagrostis arenaria* (marram grass). In Australia, invasive alien *Thinopyrum junceiforme* (sea wheatgrass) is able to take advantage of increased soil salinity (Hilton *et al.*, 2006).

Sea level rise could also drive the intentional introduction of invasive alien species for the purposes of climate change adaption to reduce impacts of coastal erosion and infrastructure damage. For example, *Sporobolus* species, introduced to reduce the effects of coastal erosion (Ge *et al.*, 2015), have become widespread invasive alien species in China (An *et al.*, 2007). The introduction of *Calamagrostis arenaria* (marram grass) in Australia and New Zealand are further examples of alien species introduced for dune stabilization for coastal protection. The need for improved coastal protection from rising sea levels could see alien species being utilized in many parts of the world. Alternatively, the construction of hard surfaces for coastal protection against sea level rise can also facilitate the establishment of invasive alien species of seaweed (Geraldi *et al.*, 2014).

3.3.5 Invasive alien species

Although studying the role of invasive alien species as a direct driver of change in nature affecting invasive alien species might sound like circular reasoning, there is increasing evidence of the role that invasive alien species may play in facilitating other alien species **(Figure 3.21)**. The process by which facilitation among alien species potentially accelerates the accumulation of introduced species has gained its own term, "invasional meltdown" (Simberloff, 2006; **Chapters 1**, **2**, **4**).

3.3.5.1 Biotic facilitation

Invasive alien species can facilitate the establishment and spread of other invasive alien species through multiple direct and indirect ecological interactions **(Box 3.10)**. Direct biotic

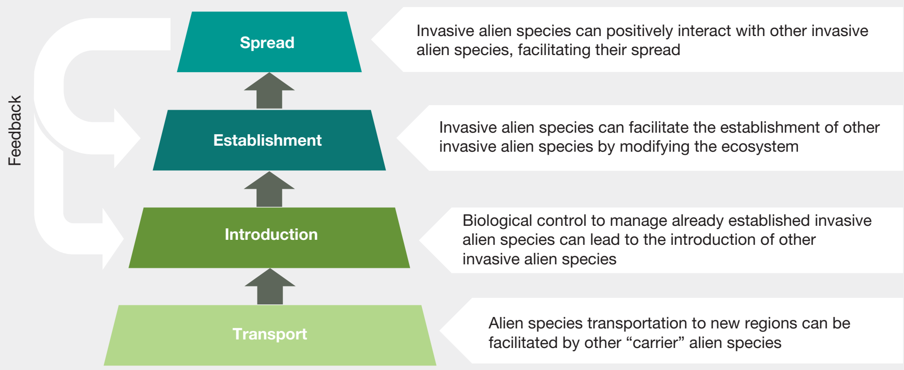


Figure 3 21 **Examples of the role of invasive alien species in facilitating additional invasive alien species across stages in the biological invasion process.**

Invasive alien species may facilitate further biological invasions by acting as pathways for other invasive alien species, by motivating the deliberate introduction of additional alien species for biological control, by modifying the ecosystem thereby facilitating the establishment other alien species, or by facilitating spread. Biological invasions can also negatively impact ecosystem functioning and resistance, causing feedback *via* facilitation of the introduction and establishment of additional invasive alien species.

facilitation often involves plant-animal interactions (e.g., pollination; e.g., Morales & Aizen, 2002), dispersal, (e.g., Mandon-Dalger *et al.*, 2004), plant-fungal interactions (e.g., mycorrhizal symbiosis; Dickie *et al.*, 2010), or animal-animal (e.g., ant-scale insect) mutualisms (Richardson, Allsopp, *et al.*, 2007; Simberloff & Von Holle, 1999; Traveset & Richardson, 2014), or even multitrophic interactions like those between alien herbivores dispersing alien fungi (e.g., mycorrhiza of alien trees; Nuñez *et al.*, 2013). However, alien species may also indirectly facilitate the establishment and spread of other invasive alien species, by modifying the biotic conditions of the recipient community (e.g., reducing competition or predation pressure by a third species, or increasing food resource availability), or abiotic attributes and ecosystem properties (e.g., by promoting habitat disturbance such as enhanced fire regimes; see **section 3.3.4.5**) increasing soil nutrients by nitrogen-fixing plants, etc.

The term "invasional meltdown" coined by Simberloff & Von Holle (1999), refers to the process by which alien species facilitate one another, magnifying ecological effects, leading to accelerating rates in the number of invasive alien species and magnification of impacts. In other words, invasional meltdown is the potential emergent result of a series of facilitations (Ricciardi, 2001). Therefore, although invasional meltdown has often been broadly used to refer to any kind of positive interaction among alien species in the peer-reviewed literature, this chapter refers to invasional meltdown *sensu* (Simberloff & Von Holle, 1999), and shows how this phenomenon is linked to facilitation among invasive alien species as a driver that may accelerate rates of biological invasions (**Chapter 2**), and synergistic impacts (**Chapter 4**).

A recent review based on 150 empirical studies, Braga *et al.* (2018), confirmed overall broad support for facilitative interactions among alien species (63.3 per cent of the studies) across multiple types of interactions (direct or indirect, unidirectional, reciprocal, or multi-species), ecological levels (individual, population, community and ecosystem), taxonomic groups and major habitat types. This evidence points to biotic facilitation among alien species as a major driver facilitating the establishment and spread of invasive alien species. However, they also found some exceptions to this general pattern, and have identified biases and gaps (see below). This section reviews the role of biotic facilitation among alien species as a driver affecting the different stages of the invasion process (Braga, Gómez-Aparicio, *et al.*, 2018; Gavira-O'Neill *et al.*, 2018; Jeschke *et al.*, 2012).

The transportation of alien species to new regions can be facilitated by other "carrier" alien species. For instance, plants relying on endozoochoric or ectozoochoric seed dispersal can be transported and introduced to new regions in the guts, fur, hoof or feathers of alien animals (Reynolds *et al.*, 2015; Van Leeuwen, 2018; Diaz Velez *et al.*, 2020). The alien mammal *Axis porcinus* (hog deer) disperses similar numbers of alien and native plant species' seeds through its faeces, thus greatly facilitating the dispersal of alien species in south-eastern Australia (N. E. Davis *et al.*, 2010), and horses transport alien seeds on their hooves (Gower, 2008). Indeed, facilitation is concomitant

Box 3 10 Three-way invasional meltdown: invasive alien ungulates disperse invasive alien fungi that facilitate pine invasions.

One example of invasional meltdown that involves belowground mechanisms of facilitation, is that of alien ungulates dispersing alien ectomycorrhizal fungi, in turn facilitating the invasion by alien pine trees **(Figure 3.22)**. Introduced pine trees have become invasive in many parts of the southern hemisphere and cause profound ecological, social and economic impacts. Pine tree establishment and growth are critically dependent on the interaction with ectomycorrhizal fungi, which provide nutrients, water and protection against pathogens, in exchange for plant carbon. Pine trees thus co-invade with alien ectomycorrhizal fungi. As ectomycorrhizal fungi disperse independently from pine trees, some ectomycorrhizal fungi species are able to disperse away from the original place of introduction, establish a spore bank, and make stands of native species more susceptible to pine invasions. In turn, invasive alien ungulates consume alien ectomycorrhizal fungal sporocarps and disperse the spores of some ectomycorrhizal fungi species through their faeces (Nuñez *et al.*, 2013). This mechanism of dispersal is crucial for the pine-ectomycorrhiza symbiosis both in the alien and native ranges fungi, especially for those ectomycorrhizal fungi that produce hypogenous sporocarps (i.e., truffle-like fungi), which are proposed to exclusively rely on mammal-mediated dispersal **(Figure 3.22)**. Invasive ungulates can disperse viable spores in high densities, far beyond the distance they typically disperse through wind (Horton, 2017). This scale of dispersal is important considering the scale at which biological invasion occurs. Although not all ectomycorrhizal fungi species survive this form of dispersal, evidence shows that those ectomycorrhizal fungi species that survive or even depend upon mammal-mediated dispersal are among the most invasive ectomycorrhizal fungi (Policelli *et al.*, 2019). Dispersal limitation of ectomycorrhizal fungi might be determinant for invasions of Pinaceae. The absence of dispersal vectors, such as ungulates, could act as an impediment for viable ectomycorrhizal fungi propagules to reach sites far from the propagule source, in turn hindering the invasion by the alien plant host or increasing its lag time.

Box 3 10

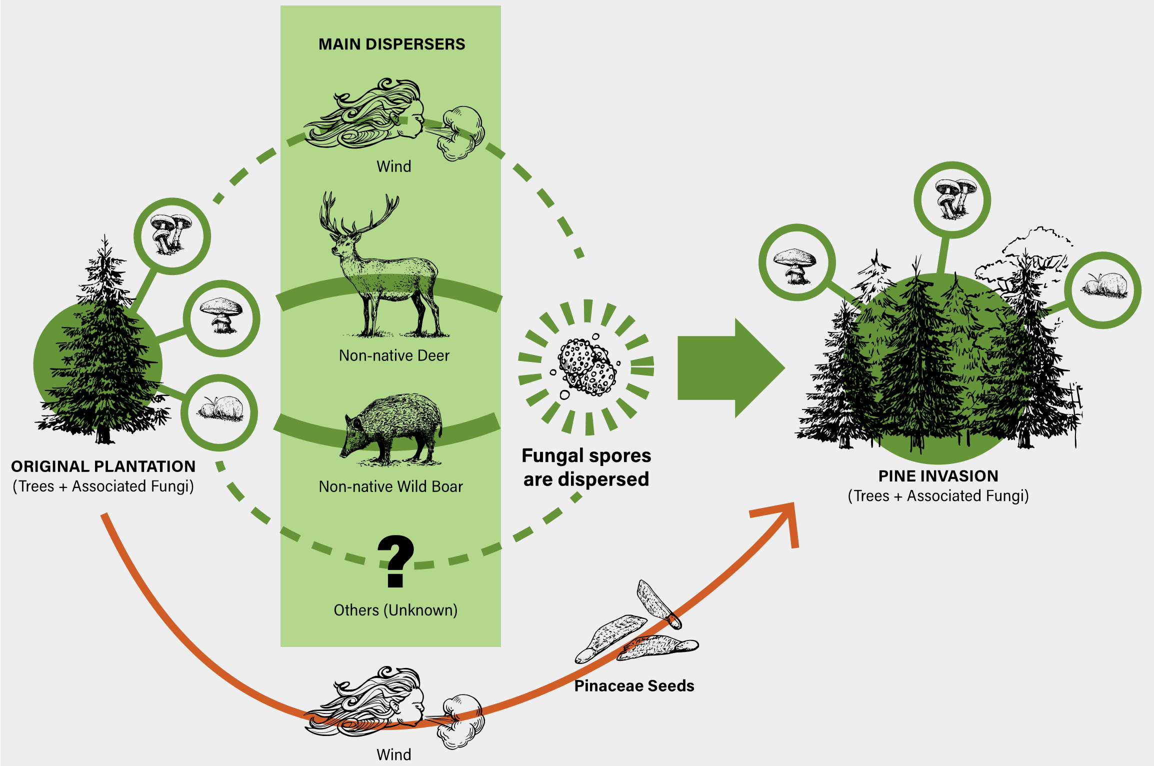


Figure 3 22 **Diagram of the three-way invasional meltdown between invasive alien pine trees, invasive alien ectomycorrhizal fungi and invasive alien ungulates.**

Pine trees need ectomycorrhizal fungi to successfully invade (thick middle arrow). Pine seeds are mainly dispersed by wind (bottom arrow). Spores from ectomycorrhizal fungi can be dispersed through wind (upper dotted line) but some ectomycorrhizal fungi species present in the pine plantation produce sporocarps that are eaten by invasive alien ungulates (wild boar and deer; medium thick lines). Ungulates transport the invasive ectomycorrhizal fungi spores further from the invasion source population compared to wind. Spores from some invasive ectomycorrhizal fungi can form long-lasting spore banks in the soil, making native stands more susceptible to pine invasion. More evidence is needed about other potential mechanisms of fungal dispersal (here represented by the question mark, lower dotted line), such as bird dispersal, or human dispersal which could also be important, especially over long-distances. Source: Policelli *et al.* (2022), under license CC BY 4.0. https://doi.org/10.1007/978-3-031-12994-0_2

with the uptake, transportation and introduction of invasive alien species that engage in obligated symbiosis with other organisms and in the co-introduction of alien parasites by their alien hosts (e.g., Arbetman *et al.*, 2013). As an example, frugivorous birds have been shown to simultaneously disperse three interlinked alien species: the seeds of *Ligustrum lucidum* (broad-leaf privet), its weevil granivore and a parasite of the weevil (Chen *et al.*, 2021). However, despite the importance of transport and introduction within biotic facilitation **(Figure 3.4)**, these initial two stages of the biological invasion process have been largely neglected in major studies and reviews about facilitation among invasive alien species or invasional meltdown (O'Loughlin & Green, 2017; Simberloff, 2006; Simberloff & Von Holle, 1999).

Once alien species have arrived in a new region, positive interactions with other alien species may be unidirectional or bidirectional. Unidirectional interactions include alien species facilitating any aspect of another's survival, reproduction, resource acquisition, or other factor that enhances establishment, population growth, or spread while the latter has no detectable influence on the former (a commensal relationship). With bidirectional interactions, both species have a reciprocal positive effect (mutualism). Multispecies interactions may be through direct and/or indirect effects (reviewed in (Braga, Gómez-Aparicio, *et al.*, 2018). According to Braga *et al.* (2018), most studies focused on unidirectional or multi-species interactions (58 studies each) and these generally found a high level of support for facilitation, while there were fewer studies on reciprocal interactions (34 studies) and these generally found a lower level of support for facilitation (Braga, Gómez-Aparicio, *et al.*, 2018). As an additional scenario, one alien species could facilitate the success of another at its own expense, such as through a predator-prey or parasite-host relationship; such exploitations are likely quite common, but are also rarely considered in studies examining facilitations (but see Grosholz, 2005; Ricciardi, 2001). Empirical evidence exists for multispecies interactions that affect the success of an invasive alien species or trigger the expansion of an alien species. For example, Grosholz (2005) showed that the invasion by a predator, *Carcinus maenas* (European shore crab), reduced the abundance of a native clam, which was the crab's preferred prey, by 10-fold,; this interaction released another introduced species, *Gemma gemma* (amethyst gemclam), from competition and thus allowed it to become superabundant, after having been present at low abundance for decades. However, while many studies have inferred invasional meltdown, few cases have demonstrated an accelerating rate of establishment or spread of invasive alien species and/or the synergistic impact of these invasive alien species. Heimpel *et al.* (2010) described a scenario of invasional meltdown where *Aphis glycines* (soybean aphid) increased the abundance of eleven invasive alien species including worms, shrubs, birds, beetles and animal and plant pathogens. A study by Ricciardi (2001) of the North American Great Lakes found that facilitative interactions among alien species were at least as common as antagonistic interactions, and that the rapid accumulation and synergistic effects of alien species, while best explained by increased propagule pressure (e.g., from shipping), was consistent with the prediction of the invasional meltdown hypothesis (Simberloff & Von Holle, 1999). Christmas Island, mentioned previously, provides the best documented case of invasional meltdown to date. After being introduced to the island several decades ago, *Anoplolepis gracilipes* (yellow crazy ant), persisted for decades at low density before its population exploded in the late 1980s. The ants had an antagonistic relationship with *Gecarcoidea natalis* (Christmas Island red crab), a keystone omnivore. The ants caused a reduction in populations of the crab, which resulted in increased tree seedling density and reduced leaf litter on the forest floor. Further, the depletion of *Gecarcoidea natalis* promoted yet another invasive alien species, *Lissachatina fulica* (giant African land snail). Simultaneously, in the forest canopy, the higher density of ants promoted population growth of introduced honeydew-secreting scale insects through a mutualistic relationship, which resulted in fungal growth and dieback of trees. This ecosystem transformation occurred in a period of only a few years (Green *et al.*, 2011; O'Dowd *et al.*, 2003).

Finally, Braga *et al.* (2018) identified biases in research effort. In particular, the majority of the studies focused on the individual and population levels (about 44 per cent each), with a lower representation of studies at the community (10.5 per cent) and ecosystem levels (1.5 per cent), and there are less studies addressing indirect effects (56 studies) than direct effects (87 studies). Regarding habitats, most evidence comes from terrestrial ecosystems (63.1 per cent) compared to fresh and marine ecosystems (21.5 and 15.4 per cent, respectively). As for taxonomic groups, more studies focused on plants and algae (89 studies), followed by invertebrates (83 studies) and vertebrates (51 studies). In the future, taking the importance and prevalence of alien-alien facilitation into account might lead to better prediction of the outcomes of biological invasions and effective prevention (**Chapter 5**). Moreover, while there have been many examples of invasive alien species facilitating one another, suggesting that invasional meltdown is possible in a broad range of ecosystems, there is thus far very little published evidence of an accelerated accumulation of invasive alien species attributable to these facilitations (but see O'Dowd *et al.*, 2003; Ricciardi, 2001; Simberloff & Von Holle, 1999).

3.3.5.2. Unintended consequences of management through biological control

Many empirical examples of the unintended consequences of management of biological invasions resulting in the introduction, establishment or spread of invasive alien species stem from the literature on early attempts at biological control (**Chapter 5**, **section 5.6.2.3**). Many of these historical high-profile cases report negative direct impacts on non-target native species by generalist predators or pathogens released as biological control agents (e.g., the release of cats and mongoose to control rodents, cane toads against agricultural pests and plant pests or diseases to control invasive plants). These examples are all from a time when biological control was implemented in an unregulated way, for example, with no requirement for risk assessment of the biological control agent (**Chapter 5**). A classic example is *Cactoblastis cactorum* (cactus moth) that was intentionally released on islands in the Caribbean in 1957 for the control of native *Opuntia* (pricklypear) species that were seen as a nuisance to tourists. However, the moth spread from the Dominican Republic to Florida, where it poses a threat to native *Opuntia* (Hinz *et al.*, 2019), and to the Yucatán peninsula where it was successfully eradicated (Senasica, 2019). It has currently spread across the south-eastern United States to Texas where it can enter Mexico again and threaten the over 100 native *Opuntia* species, many of which are endemic and constitute an important part of the Mexican diet and economy (Senasica, 2019).

Insects have also been released to control other insects and in some cases these biological control agents have become invasive alien species. Examples include two species of ladybird, *Harmonia axyridis* (harlequin ladybird) from Asia causing declines of native ladybirds in the United Kingdom and Belgium (Roy *et al.*, 2012) and in other countries worldwide (Roy *et al.*, 2012) and *Coccinella septempunctata* (seven-spot ladybird) from Europe impacting populations of native North American ladybirds (E. W. Evans *et al.*, 2011). The release of *Euglandina rosea* (rosy wolf snail) in Hawaii to control *Lissachatina fulica* (giant African land snail) also failed to lead to desired management outcomes but instead resulted in the intentional introduction of an invasive alien species (Cowie, 2001).

Rhinella marina (cane toad) was introduced into Queensland, Australia in 1935 from Hawaii to control insect pests of sugar cane and became an invasive alien species with direct and possible indirect impacts on non-target native Australian vertebrates (R. Shine, 2010). This is an example where science was ignored and a political decision was made to introduce *Rhinella marina* (M. D. Day *et al.*, 2021). Mammals have also been released as biological control agents with unintended consequences. *Herpestes javanicus auropunctatus* (small Indian mongoose) was introduced initially to control alien invasive rodents and snakes in the West Indies, Hawaiian islands and Japan, and has resulted in mammal and reptile extinctions (Hays & Conant, 2007). In aquatic environments, *Gambusia affinis* (western mosquitofish) and *Gambusia holbrooki* (eastern mosquitofish), native to the fresh waters of the United States, have been introduced worldwide as biological control agents of mosquito larvae, but are implicated in the decrease and loss of non-target native invertebrates as well as fish and amphibian populations (Azevedo-Santos *et al.*, 2017). In the marine realm, the sea urchin *Evechinus chloroticus* (kina) released as an augmentative biological control agent against the invasive *Undaria pinnatifida* (Asian kelp) showed substantial non-target effects on benthic communities, however these were localized and reversible (Atalah *et al.*, 2013). Conservation actions may also have unintended consequences in facilitating invasive alien species, as illustrated by the creation of beaver dams during the reintroduction of *Castor canadensis* (North American beaver) in Verde River, Arizona, United States, which shifted desert fish assemblages toward dominance by alien species (P. P. Gibson *et al.*, 2015; Reaser, 2003).

A global review of non-target impacts of weed biological control agents found that the proportion of intentionally released biological control agents causing non-target effects declined from 18.2 per cent prior to the 1960s to 9.9 per cent in the period 1991–2008 (Hinz *et al.*, 2019). Similarly, an analysis of all non-target effects of weed biological control programmes from 1969 to 2014 showed a risk factor of less than 1 per cent (Moran & Hoffmann, 2015). There was no evidence of non-target impacts from plant pathogens used for biological control (Suckling & Sforza, 2014).

3.4 ADDITIONAL DIRECT DRIVERS – NATURAL DRIVERS AND BIODIVERSITY LOSS

3.4.1 Natural hazards

Natural large-scale disturbances, such as hurricanes, earthquakes and tsunamis can facilitate the onward spread of alien species from an existing invaded range to new regions (Carlton *et al.*, 2017; **section 3.3.3.3**, **Box 3.8**) as well as encourage their wider spread within regions where they are already present as aliens (Bellingham *et al.*, 2005; **Figure 3.23**). Natural drivers have thus facilitated the wider establishment and spread of alien plants and animals within and beyond their known invaded range through acting as agents of secondary dispersal (e.g., Lovette *et al.*, 1999; Toepfer, 2012; Lee *et al.*, 2014; Massa *et al.*, 2014).

The roles of natural drivers apply to all regions and all realms. Natural disturbances such as hurricanes (**section 3.3.4.3**) have played a role in assisting the dispersal of alien animals (Andraca-Gómez *et al.*, 2015; Censky *et al.*, 1998; Johnston & Purkis, 2015), plants (Bhattarai & Cronin, 2014) and microbes (Feehan *et al.*, 2016), leading to expansion of their historical invaded ranges. A classic example of onwards dispersal of alien species *via* natural drivers is the crossing from Africa to the Americas by the *Bubulcus ibis* (cattle egret), whose introduction, establishment and further spread throughout the Americas has been linked to multiple weather events (Massa *et al.*, 2014). Wind and ocean currents offer new opportunities for colonization within and beyond the invaded range of both marine and terrestrial organisms (Munoz *et al.*, 2004); rafting during extreme weather events is a common example by which non-flying alien animals can be transported between islands, as has been documented for *Iguana iguana* (iguana; Censky *et al.*, 1998). As species' thermal barriers are being altered or lifted by climate change, ocean currents are contributing to the range expansion of alien species and colonization of previously inhospitable regions such as the Arctic (Chan *et al.*, 2019) and Antarctica (C. I. Fraser *et al.*, 2018). Disease outbreaks among *Strongylocentrotus droebachiensis* (green sea urchin) in the northwest Atlantic Ocean have been attributed to *Paramoeba invadens*, a pathogenic amoeba that is intolerant of the typical winter sea surface temperatures in the region. Evidence suggests that the amoeba originates in southern surface waters transported to the north Atlantic coast, and that disease outbreaks have occurred during hurricanes and unusual warm winter sea temperatures (Feehan *et al.*, 2016). Molecular and oceanographic evidence suggests that ocean currents regularly disperse rafting species thousands of kilometres, and that Southern Ocean coasts are biologically well-connected (C. I. Fraser *et al.*, 2022). If warm-adapted

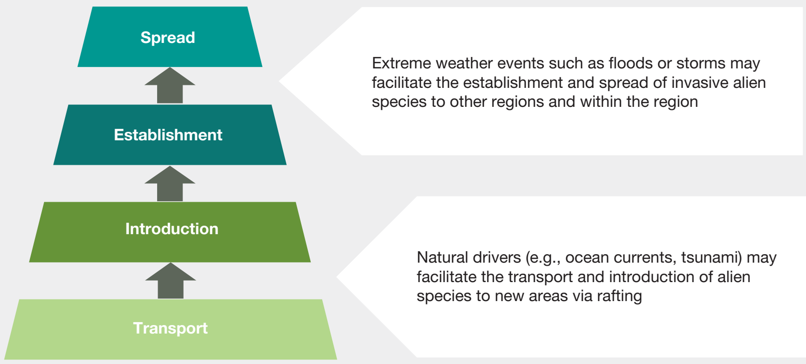


Figure 3 23 **Examples of the role of natural hazards in facilitating invasive alien species across stages of the biological invasion process.**

Natural hazards can facilitate biological invasions by acting as agents of secondary dispersal beyond and within the invaded range. Examples are chosen to represent relationships found across the invasion stages.

taxa frequently disperse to Antarctic waters, global warming could allow the region to become increasingly colonized by new species delivered *via* ocean rafting, especially during storms (C. I. Fraser *et al.*, 2018). These cases illustrate the capacity of natural drivers to facilitate colonization events, but also suggest an increasing influence of anthropogenic climate change as an amplifier of such dispersal opportunities, by, for example, altering or strengthening ocean currents, or by creating temporary hydrological connections (**section 3.3.4**).

The relative importance of natural drivers such as natural hazards in the range dynamics of alien species, however, are likely to be relatively minor. Natural long-distance dispersal events have evidently been sufficient to colonize remote oceanic islands in the prehistoric past, but are likely orders of magnitude less frequent than human-assisted, long-distance dispersal events (Ricciardi, 2007). Natural hazards typically move small numbers of propagules and are dependent on weather patterns and other environmental constraints. This is in contrast to modern human-assisted biological invasions in which enormous numbers of individual organisms and a broad diversity of species can be moved to virtually any region of the planet over short time scales (Ricciardi, 2007). The spread of alien species often involves a combination of human-assisted and natural drivers, of which the latter may be dominant at small spatial scales (Chan *et al.*, 2019; Medley *et al.*, 2015).

3.4.2 Biodiversity loss and ecosystem resilience

It is estimated that 25 per cent of all species globally are threatened by extinction and that 1 million species may become extinct in the following decades due to human interference, especially land- and sea-use change (**section 3.3.1**) and direct exploitation of natural resources (**section 3.3.2**) (IPBES, 2019). While this biodiversity loss has been the dependent variable in most previous IPBES assessments (IPBES, 2019), for invasive alien species it can also be seen as a driver that may facilitate biological invasions since reduced taxonomic or functional diversity of native ecosystems may reduce their biotic resistance and thereby facilitate the establishment and spread of invasive alien species (Levine *et al.*, 2004; **Figures 3.3** and **3.24**). A wide range of biotic interactions may confer resistance to biological invasions in native communities, including competition, predation, herbivory and disease, and all of these may be involved in constraining the introduction, establishment and spread of invasive alien species (Alofs & Jackson, 2014; Elton, 1958; Levine *et al.*, 2004).

Studies from terrestrial systems show that the presence and diversity of native vegetation, along with phylogenetic distance between the invasive alien species and resident community, can constrain plant invasions, implicating different modes of plant-plant competition for space as a powerful mechanism underlying biotic resistance to invasive alien species. For example, Byun *et al.* (2015) analyzed the interplay between abiotic constraints, propagule pressure and biotic resistance by conducting experiments to explore the *Phragmites australis* (common reed) invasion process, and found that maintaining native plant cover could confer invasion resistance, even when abiotic conditions changed (Byun *et al.*, 2015). Going *et al.* (2009) found that competition from a resident annual plant community had strong negative effects on the biomass and reproduction of invasive alien grass, such as *Avena barbata* (slender oat), *Bromus diandrus* (great brome) and *Hordeum murinum*

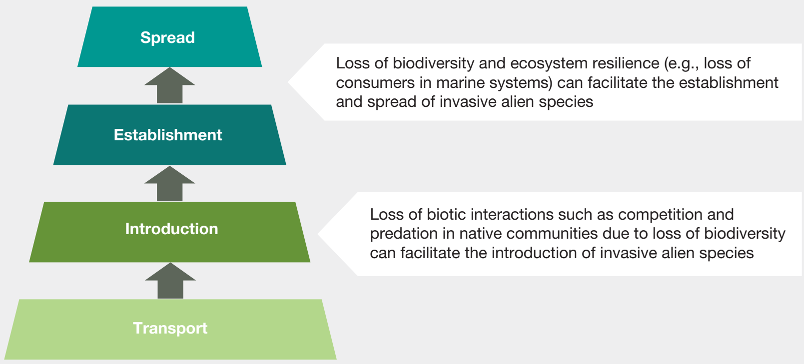


Figure 3 24 **Examples of the role of biodiversity loss in facilitating invasive alien species across stages of the biological invasion process.**

Biodiversity loss can facilitate biological invasions by reducing ecosystem resistance to invasion, which may facilitate the introduction, establishment and spread of invasive alien species.

(mouse barley), and that removing the resident communities increased the biomass and seed production of the invasive alien species by two-fold to ninefold. Elton's diversity-invasibility hypothesis proposes that taxonomic diversity in native communities confers additional resistance to invasive alien species because less niche space is available to alien species (Elton, 1958). In support of this hypothesis, Maron & Marler (2007) found that plant assemblages with higher plant species richness displayed lower invasibility (**Chapter 1**, **section 1.3.2**) than assemblages with lower species richness, and Zheng *et al.* (2018) found that the invasion success of *Chromolaena odorata* (Siam weed) correlated negatively with both biomass and species richness of the native community. A third idea related to biotic resistance is Darwin's naturalization hypothesis, which builds on Darwin's (1859) position that alien species will be more successful in a native community if they are more distantly related to native residents, because relatedness may indicate niche similarity (**Chapter 1**, **section 1.3.2**; Violle *et al.*, 2011). In support of this hypothesis, Zheng *et al.* (2018) experimentally established that success of the invasive tropical shrub *Chromolaena odorata* increased with functional distance to the native community. Similarly, Iannone *et al.* (2016) found, in a large-scale observational study of invasive alien species in forests across the eastern United States, that tree biomass and evolutionary diversity, but not species richness, was negatively associated with the establishment and dominance of the invasive alien species, and thus that evolutionary diversity is indicative of biotic resistance. In an experimental study explicitly designed to distinguish Darwin and Elton's hypotheses, Feng *et al.* (2019) found support for both ideas, as the effects of both phylogenetic and functional distance became stronger as species richness increased, and further analyses indicated that both competitive inequalities and niche differences between invasive alien and native communities may contribute to these responses.

Observed relationships between the taxonomic or functional diversity of native and invasive alien plants may be caused by mechanisms beyond direct plant-plant competition. For example, observed biotic resistance from native vegetation against invasive alien plant species may operate *via* soil pathogens that negatively affect the invasive alien species (Knevel *et al.*, 2004; van Ruijven *et al.*, 2003). Similarly, a study from south-western United States by St. Clair *et al.* (2016), found that native rodents suppressed invasion by *Bromus tectorum* (downy brome) while promoting native plant diversity after fire, providing strong biotic resistance to invasive alien plants through preferential seed and seedling predation on invasive alien species.

A meta-analysis of marine experiments revealed the same general trend of diversity-mediated biotic resistance as was observed in terrestrial systems; high native primary producer diversity in marine systems confers significant resistance to alien primary producers through competition, whereas low-diversity communities in the same marine systems often fail to do so (Kimbro *et al.*, 2013). However, unlike terrestrial systems, biotic resistance in freshwater and marine environments might to a larger extent be driven by consumption (Alofs & Jackson, 2014). Resident species at the top of the food chain can prevent invasion by alien species which are lower in the food chain. In freshwater systems in the southern United States, Parker & Hay (2005) found that native consumers (including crayfish, grasshoppers and slugs) preferred alien plants as a food source over native plants, conferring resistance to biological invasion. In another example, in China the native crab *Helice tientsinensis* effectively inhibits *Sporobolus* *alterniflorus* (smooth cordgrass) invasion in anthropogenic ditches, high marshes and estuarine mangrove forest by grazing seedlings and suppressing their density and survival (Ning *et al.*, 2019). In rainforest of Christmas Island, Indian Ocean, *Gecarcoidea natalis* (Christmas Island red crab) can kill the introduced *Lissachatina fulica* (giant African land snail), restricting the distribution of giant African land snails and thus conferring biotic resistance to biological invasions in undisturbed habitats on the island (Lake & O'Dowd, 1991).

3.5 MULTIPLE, ADDITIVE OR INTERACTING EFFECTS OF DRIVERS AFFECTING INVASIVE ALIEN SPECIES

The evidence that the majority of the Earth's ecosystems are subject to complex threats from several concurrent, interacting and exacerbating drivers of change in nature is unequivocal (IPBES, 2019). The net effect of drivers is often not additive, as drivers can reinforce or mitigate each other's effects (i.e., be synergistic or antagonistic; Fontúrbel, 2020; Jackson *et al.*, 2016; Pyšek *et al.*, 2020). Generalizing from studies of single drivers in isolation may therefore yield misleading conclusions (Bowler *et al.*, 2020). Interactions between multiple drivers of change are expected to jeopardize ecosystem functioning and biodiversity, and are a key concern for conservation and management (Cote *et al.*, 2016). As a special case, novel ecosystems (**Chapter 1**, **Box 1.5**), which contain new species combinations and/or altered ecosystem functioning (Hobbs *et al.*, 2006, 2009; Morse *et al.*, 2014; Seastedt *et al.*, 2008) can be more susceptible to biological invasions than more native ecosystems (Ogutu-Ohwayo *et al.*, 2016).

Associations amongst invasive alien species and other drivers of change in nature are generally understudied, and the degree to which biological invasions are affected by additive or multiplicative processes and interactions among drivers is therefore difficult to assess (**Figure 3.25**, **Chapter 1**, **section 1.3.3**). A recent review found that only 16 per cent of published research on invasive alien species examined associations with at least one other direct or indirect driver of change in nature, and less than 3 per cent considered associations with two or more additional drivers (Hulme, 2022). This section acknowledges the limited information on interactions between invasive alien species and other drivers of change in nature, and refers to a number of illustrative, rather than exhaustive, examples to highlight the importance of taking such interactions into account **(Box 3.11)**.

Indigenous Peoples and local communities recognize that most drivers of change on their lands do not act in

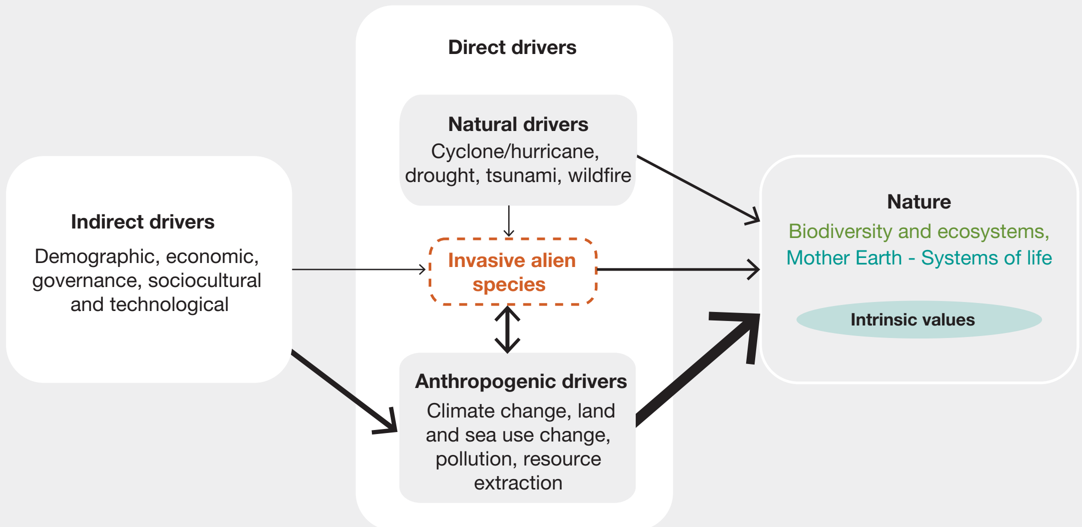


Figure 3 25 **Schematic representation of the links between indirect and direct drivers of change in nature in relation to their potential effect on invasive alien species (see Figure 3.3).**

The size of the arrows represents the available evidence in the scientific literature for the importance of the different links, as assessed though a bibliometric analysis of the literature (the absolute number of articles retrieved is reflected in the size of each arrow). Adapted from Hulme (2022), https://doi.org/10.1111/cobi.13817, under license CC BY 4.0.

Box 3 11 **Multiple interacting drivers trigger plant invasions in mountains.**

In the last two decades, evidence has highlighted the increasing number of alien plants establishing in mountain regions, despite mountains across the world differing greatly in terms of their biodiversity, climate, geology, land-use and other socioecological factors (e.g., T. Becker *et al.*, 2005; Dainese *et al.*, 2014; Guo, Fei, *et al.*, 2018; Khuroo *et al.*, 2007; Kueffer *et al.*, 2013; Marini *et al.*, 2012). In a standardized survey along elevational gradients in nine regions on four continents, more than 300 alien plant species were observed (Haider *et al.*, 2018).

Historically, agriculture and domestic grazing were probably the first and most extensive drivers that facilitated plant invasions in mountains. For example, species typical for European grasslands are widespread in the alien flora of mountains worldwide (McDougall *et al.*, 2011). However, as mountains have become more heavily developed, drivers such as infrastructure and anthropogenic land-use changes (including urbanization and the development of corridors such as roads, trails and railways) have synergistically supported the upslope movement of alien plants introduced at low and mid-elevations (Alexander *et al.*, 2011; Lembrechts *et al.*, 2017; Liedtke *et al.*, 2020; Rashid *et al.*, 2021; Yang *et al.*, 2018). Corridors provide a conduit for rapid movement of propagules aided by the continuous movement of vehicles and construction material (Rew *et al.*, 2018). Furthermore, the typically ruderal alien species benefit from the disturbed habitat conditions resulting from roadside construction and maintenance (Lembrechts *et al.*, 2016; Pickering & Hill, 2007; Seipel *et al.*, 2012).

In recent decades, and because of technological advances and higher economic and development pressures, mountain ecosystems have experienced a new phase of extensive land-use changes and infrastructure development, which has triggered the spread of invasive alien plants to even higher and more remote areas (Kalwij *et al.*, 2015; Rew *et al.*, 2018). Tourism in mountain areas has exponentially increased across the world (reviewed by Río-Rama *et al.*, 2019), increasing the development pressure in mountainous and alpine ecosystems. In most regions, there has been an increase in human settlements including housing and urbanization for tourism and recreation, as well as the expansion of infrastructure such as roads, railroads, powerlines and telecommunication towers. Overall, increasing land development, traffic and visitation rates have multiplied the chances for the introduction and establishment of invasive plant propagules at high elevations (McDougall *et al.*, 2011).

Figure 3 26 **Monte Baldo hosts an increasing number of invasive alien species.**

An increasing number of alien plants have been establishing in mountains like Monte Baldo throughout the European Alps (Dainese *et al.*, 2014). Photo credit: Katzwiekatzkann, WM Commons – under license CC BY 3.0.

Box 3 11

Climate change is expected to facilitate the expansion of invasive alien species to higher elevations both through direct and indirect effects. Climate change will reduce climatic barriers for generalist alien plants (Pauchard *et al.*, 2016), especially in regions which are not water-limited. Range shifts towards higher elevations have been reported, and alien plants appear to be moving up in elevation faster than native species (Dainese *et al.*, 2017). Increased disturbance due to, for example, higher fire frequency and intensity and insect and pathogen outbreaks triggered by climate change, will also play a role in promoting invasive alien species, especially in the middle elevations of mountains where forests will be more prone to invasion by woody plants (Franzese & Raffaele, 2017; Jactel *et al.*, 2020; Liebhold *et al.*, 2017). By reducing snow cover, climate change will promote the displacement of mountain ski facilities and resorts to higher elevations and into previously undeveloped areas. In addition, summer use of high elevation mountain resorts may be boosted in search for cooler places or "last chance tourism" (e.g., Kilungu *et al.*, 2019). The interactive effects of multiple drivers of change in nature affecting plant invasions are generally underestimated and primarily focus on climate change. However, interactions between climate change, infrastructure development, social values and land-use change will be informative because simple projections based solely on climate will be unreliable (Dainese *et al.*, 2017).

isolation in facilitating invasive alien species.[8] For instance, the interaction between economic and sociocultural drivers has been identified by Indigenous Peoples and local communities as responsible for the introduction and establishment of invasive alien species, as exemplified by the complexity and variability of societal and ecological processes facilitating the spread and establishment of *Prosopis juliflora* (mesquite; **Box 3.6**). Indigenous Peoples and local communities from Botswana, Ethiopia, Jordan and Kenya report that the main cause of the dispersal and spread of *Prosopis juliflora* is wildlife and livestock (Al-Assaf *et al.*, 2020; Bekele *et al.*, 2018; Haregeweyn *et al.*, 2013; IPBES, 2020; Mosweu *et al.*, 2013; Wakie *et al.*, 2016), which are linked to both sociocultural and economic drivers (pastoralist livelihoods). The Afar from Ethiopia now also use *Prosopis juliflora* as fuel wood, animal fodder and construction materials (Haregeweyn *et al.*, 2013) for economic reasons, which also contribute to its spread and establishment. In the Ramnad area of Tamil Nadu, India, sociocultural and land-use change led local communities to adopt charcoal-making, which promoted the spread of *Prosopis juliflora* through the reduction of grazing land and livestock holdings (Chandrasekaran & Swamy, 2016). Similar observations have been made for other species. For example, Indigenous Peoples and local communities in Ghana, West Africa and Himalayan India have observed the invasion of *Chromolaena odorata* (Siam weed; Amanor, 1991). Most of the Indigenous Peoples and local communities identify multiple drivers, such as the movement of humans and machinery, trade, land-use change, infrastructure development such as road construction and tourism, as important in facilitating the spread of this invasive alien species on their lands (Amanor, 1991; Braimah & Timbilla, 2002; Kosaka *et al.*, 2010; Timbilla & Braimah, 1993; Uyi & Igbinosa, 2013).

8. Data management report available at: https://doi.org/10.5281/zenodo.5760266

3.5.1 Land-use change and climate change

Most of the current knowledge on interactive effects of climate change and land-use change on biological invasions is informed by modelling studies designed to assess potential changes in species' distribution, with few experimental studies examining mechanisms based on demographic responses (e.g., L. C. Ross *et al.*, 2008). Modelling studies suggest that the relative importance of land-use change and climate change in facilitating biological invasions is highly variable and often species-specific or scale dependent (Febbraro *et al.*, 2019; Manzoor *et al.*, 2021). A general insight emerging from this work is that incorporating land-use change scenarios into climate change models can considerably alter the predicted outcomes of future biological invasions.

Climate change acts over broad regional and temporal scales, whereas land-use changes can have a much more local and immediate effect in response to commercial or land management decisions. For example, at the global scale, the future distribution of two major invasive alien plant species depended primarily on how their niches responded to climatic changes, with land-use change having a minor effect on distribution at this scale (Gong *et al.*, 2020). However, at smaller scales, several studies show that while future changes in temperature or precipitation patterns will exert a large influence on the establishment and spread of invasive alien plants, the rate of spread is often limited by the availability of suitable habitat (Taylor *et al.*, 2012), such as either cultivated or grazed land (J. V. Murray *et al.*, 2012; L. C. Ross *et al.*, 2008), urban areas (Nobis *et al.*, 2009) or the expansion of native ecosystems (Manzoor *et al.*, 2021). Interestingly, in some cases, the response of native vegetation to future climatic changes can enhance biological invasions. For example, a study from Wales found that the invasive forest understory shrub *Rhododendron ponticum* (rhododendron) is likely to decline under most climate and land-use scenarios, largely due to declines in coniferous forest cover, but is projected to increase under a scenario where ecosystem conservation leads to a substantial increase in coniferous forest cover (Manzoor *et al.*, 2021).

Increased fire activity may act synergistically with other climatic and land-use changes to drive the establishment and spread of invasive alien plant species (**sections 3.3.1.5.2**, **3.3.4**). For example, interactions among increased temperature, decreased precipitation and more frequent fires in recent decades have driven an upward spread of fire-adapted C4 invasive alien grasses (e.g., *Melinis minutiflora* (molasses grass)) along an elevation gradient in Hawaii (Angelo & Daehler, 2013). Higher atmospheric CO_2 levels have increased the productivity of invasive alien annual grasses in the western United States (Ziska *et al.*, 2005) and are predicted to favour the post-fire growth of African invasive alien grasses to the detriment of Australian native grasses (Tooth & Leishman, 2014). In the future, warmer minimum temperatures and other climatic changes in the western United States may also favour the establishment and spread of fire-adapted invasive alien grasses in previously unsuitable sites (Abatzoglou & Kolden, 2011; Martin *et al.*, 2015), although contractions of suitable habitat may also occur due to more extreme drought conditions (Albuquerque *et al.*, 2019). There is also concern that the interaction of climate change, fire activity and land management may promote grass-fire cycles and hence the spread of fire-adapted invasive alien grasses in disturbed forest ecosystems (Kerns *et al.*, 2020). Likewise, climate change, fragmentation and increased fire frequency have been shown to act synergistically to drive the spread of *Lantana camara* (lantana) in temperate forests in the Western Himalaya (Mungi *et al.*, 2018).

Few studies have investigated the interactions between land-use changes and climate change for invasive alien animals, invertebrates and microorganisms. Yet, the findings of existing studies often describe a prevalence of non-additive effects, reflecting those described above for plants. In an example from Italy, Febbraro *et al.* (2019), found that the potential distributions of four invasive alien squirrels (*Sciurus carolinensis* (grey squirrel), *Callosciurus finlaysonii* (Finlayson's squirrel), *Callosciurus erythraeus* (Pallas's squirrel) and *Tamias sibiricus* (Siberian chipmunk)) were reduced when the interactions between land-use and climate changes were included in models. In this case, climate-only models fail to account for lack of connectivity between habitats and limited overall habitat suitability, and may lead to an overestimate of the potential suitable habitat (Febbraro *et al.*, 2019). In Korea, the potential spread of an invasive alien insect *Thrips palmi* (melon thrips) in agricultural areas was shown to be influenced by rising temperatures in winter. Increased winter temperatures enabled a longer overwintering period, allowing the species to spread further across increasingly connected agricultural areas (Hong *et al.*, 2019).

Climate change and land-use changes may also interact by creating positive feedback loops, reinforcing biological invasions. For example, in the tropical dry forests of Bolivia experimental fires were shown to enhance the abundance of the invasive alien African grass *Megathyrsus maximus* (Guinea grass) in plots subjected to selective logging compared to unlogged areas, suggesting that increasing fire risk under climate change may interact with deforestation resulting from land-use change to promote the spread of this species (Veldman *et al.*, 2009). Similarly, in dryland areas in South Africa, degraded landscapes and road corridors invaded by alien grasses may alter the fuel characteristics sufficiently for fires to become a threat to an otherwise fire-absent vegetation type (Rahlao *et al.*, 2009, 2014). In these disturbed environments, land-use change and climate change interact to favour biological invasions.

3.5.2 Land-use change, climate change and nutrient pollution

While many studies comment upon the role of land-use change, climate change and nutrient pollution in the context of biological invasions, few explicitly capture interactions between these drivers or suggest causality for specific alien species introductions or stages of the biological invasion process. In fact, in many instances, invasive alien species are considered as a driver, rather than the response affected. In lieu of direct observations, paleoecological records may provide evidence for the interactive effects of land-use or sea-use change, nutrient pollution and climate change coinciding with an increase in invasive alien species. The analysis of a marsh sediment core spanning the last 1,100 years from Tivoli Bay in the Hudson River shows that climate shifts and other anthropogenic drivers (i.e., land-use change and nutrient input) occur simultaneously, with a fivefold expansion of invasive alien plant species such as *Typha angustifolia* (lesser bulrush), *Phragmites australis* (common reed) and *Lythrum salicaria* (purple loosestrife) (Sritrairat *et al.*, 2012). This study suggests that the increase in the number of invasive alien species is linked to European settlement impacts in this region, including higher disturbance, increased nutrients and sedimentation, along with warmer climate, however an explicit causal link between the different drivers and establishment of invasive alien species cannot be made.

A contemporary study of the seed recruitment of the invasive alien forbs *Bellis perennis* (common daisy), *Lolium perenne* (perennial ryegrass), *Poa pratensis* (smooth meadow-grass), *Taraxacum officinale* (dandelion), *Trifolium pratense* (red clover) and *Trifolium repens* (white clover) beyond their current invaded range in the subarctic Andes found that the species produce more biomass and flowers at higher nutrient levels and warmer temperatures and establish, grow and flower more in disturbed habitats than in undisturbed habitats (Lembrechts *et al.*, 2016). The study found no differences between the responses of these species when expanding in their invaded range in the Andes compared to expanding in their native range in the Scandes, suggesting that both plant invasions and natural range expansions in cold-climates are likely to increase with a combination of warmer climate, increased disturbance and increased nutrients (Lembrechts *et al.*, 2016).

In aquatic systems, the invasive alien *Phragmites australis* (common reed) is expanding throughout the Great Lakes of the United States (Great Lakes Phragmites Collaborative,

Box 3 12 Land-use change, climate change and nutrient pollution interact to drive the introduction, establishment and spread of *Pontederia crassipes* across Africa.

Pontederia crassipes (water hyacinth) is a fast-growing floating aquatic plant native to South America that has spread throughout vital freshwater bodies and wetlands of Africa, North America, Europe, Asia and Oceania since the late 1800s (Navarro & Phiri, 2000). Across Africa, this species has shown true exponential expansion by spreading over a large proportion of the water bodies with infestations getting worse as there is an increase in extreme climatic events in major water bodies like Lake Victoria in East Africa, Lake Nyasa in the Nile basin (especially around Lake Tana), the Zambezi River basin in southern Africa and the Tano lagoon and River Niger in West Africa. Connectivity among diverse water bodies has further facilitated the spread of water hyacinth in the region. Its spread is linked to eutrophication emanating from poor land-use management practices and is facilitated by environmental degradation and extreme climatic (i.e., temperatures, wind and floods) events (Navarro & Phiri, 2000; Téllez *et al.*, 2008; Thamaga & Dube, 2018). These extreme events facilitate the transport and introduction of water hyacinth in many freshwater ecosystems, and are also expected to alter natural surface water flow regimes, potentially further increasing the likelihood of water hyacinth and other invasive alien species establishing and spreading (Diez *et al.*, 2012; IPBES, 2019). Water hyacinth is expected to continue expanding into suitable habitat found in African ecosystems, with the rate and extent of the spread depending on disturbance from climate change and the nutrient pollution levels of the water bodies (Diez *et al.*, 2012; IPBES, 2019; Navarro & Phiri, 2000).

Figure 3 27 ***Pontederia crassipes* (water hyacinth) in Lake Victoria, Kisumu, Kenya.**

The free-floating invasive alien plant hinders small boats from docking and prevents fishing activities along the landing beaches. Photo credit: Mwe17, WM Commons – under license CC BY-SA 4.0.

2022), with its introduction, establishment and spread promoted by road networks, agricultural activities that increase nutrient availability and climate change (Mazur *et al.*, 2014). In Lake Victoria, Africa, the distribution of the invasive alien *Pontederia crassipes* (water hyacinth) rapidly expanded during the 1980s, a period linked to eutrophication and climate warming (Hecky *et al.*, 2010; Ogutu-Ohwayo *et al.*, 2016; A. E. Williams *et al.*, 2005; **Box 3.12** . While currently its spread is reduced, fears remain that land-use changes in the catchment area, along with continued nutrient loading and climate warming, will result in a resurgence of water hyacinth **(Box 3.12)**. In the late 1980s, the Baltic Sea experienced a bloom of *Mnemiopsis leidyi* (sea walnut) and a collapse of anchovy stocks, both of which were linked to a complex interaction of increased eutrophication, a changing regional climate with more severe winters and fishing pressures (Oguz *et al.*, 2008). Changing salinity arising from the new Suez Canal (**section 3.3.1.3**, **Box 3.7**) opening in conjunction with climate change is facilitated the expansion of *Brachidontes pharaonis* (variable mussel)'s distribution across the Mediterranean Basin, with this expansion also being enhanced by eutrophication associated with local urbanization (Sarà *et al.*, 2018).

3.5.3 Trade, urbanization and land-use change

Although international trade can directly introduce invasive alien species in ballast water, contaminants of commodities or stowaways in containers (**section 3.2.3.1**), it also interacts with other drivers facilitating biological invasions including: direct exploitation of natural resources, pollution, climate change, land-use change and urbanization **(Figure 3.28)**. To illustrate aspects of these interactions, the following section examines the implications of the interactions between trade, land-use change and urbanization.

International trade is an important driver of urbanization since it encourages the agglomeration of economic activities (and hence labour) in specific urban areas, particularly areas that are associated with international transport hubs such as marine ports, airports or national borders (Tripathi, 2020). Cities that have a high number of global trade links tend to be highly urbanized and urbanization also increases with the level of agricultural imports and with exports of non-agricultural commodities (Thia, 2016). Urban areas also represent hotspots of alien species richness, which in part can be explained by the high rate of intentional introductions of alien species

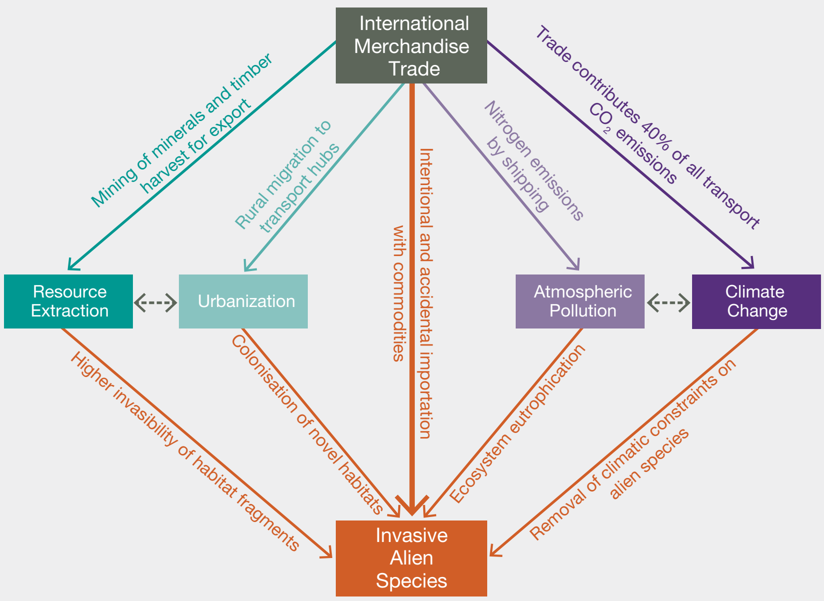


Figure 3 28 **Schematic illustration of how international merchandise trade interacts with other drivers of change in nature to influence the introduction and spread of invasive alien species.**

The thick arrow indicates the direct influence of international merchandise trade on invasive alien species, and thin arrows indicate how international merchandise trade affects other drivers which again may facilitate the introduction and spread of invasive alien species. Dotted lines represent interactions among drivers of change in nature. Adapted from Hulme (2021b), https://doi.org/10.1016/j.oneear.2021.04.015, under license CC BY 4.0.

either for amenity value (e.g., street trees) or as pets (e.g., parrots) that subsequently escape, but also by the higher international connectivity of large cities that facilitates unintentional introductions of alien species *via* ports and airports (Shochat *et al.*, 2010). In the marine realm, urbanized maritime infrastructure associated with ports (e.g., breakwaters, jetties and seawalls) does not function as a surrogate for natural rocky habitats but instead facilitates the establishment and spread of alien species (Bulleri & Chapman, 2010; **section 3.3.1.4**). For example, in coastal North America approximately 90 per cent of the alien species inhabiting hard artificial substrata have been reported from docks and marinas (Mineur *et al.*, 2012). Similarly, it can be expected that urbanization driven by international trade will lead to further development of land-based transport infrastructure such as rail and roads which may also facilitate the spread of alien species beyond the initial port of entry. The growth of urban areas also results in land-use change as natural and agricultural areas are fragmented and converted to housing. This environmental disturbance favours the persistence of generalist human-commensal species from around the world (Gavier-Pizarro *et al.*, 2010).

The extensive clearing of tropical forests in recent decades is in part driven by increased international trade in agricultural commodities and this trend is expected to continue due to further trade liberalization (Schmitz *et al.*, 2015). Increasing global demands for meat, animal feed and oil seed products have led to major changes in land-use in developing countries (Pendrill *et al.*, 2019). There is also a link between international trade in wood products (particularly roundwood timber) and declining national forest stocks, especially in developing countries in the tropics such as Indonesia and Cameroon (Kastner *et al.*, 2011). In addition, international trade increases demand for new products as in the case of the expansion of oil palm plantations in Latin America, which has occurred at the expense of other land-uses including tropical forests (Furumo & Aide, 2017). The resulting fragmentation of tropical forests also increases their vulnerability to biological invasions (Waddell *et al.*, 2020). Furthermore, new crops such as *Elaeis guineensis* (African oil palm) can themselves spread beyond cultivated areas to become invasive alien species in regions where they are not native (Zenni & Ziller, 2011).

3.5.4 Urbanization and pollution

Urbanization and pollution interact to facilitate biological invasions; invasive alien species are disproportionally found in urbanized areas with higher pollution compared to less polluted urban areas or polluted natural ecosystems. While urbanization promotes the transport and introduction and of invasive alien species both intentionally and unintentionally (**section 3.2.2.4**), pollution contributes to improve the chances of establishment and spread of an invasive alien species, which tend to be facilitated by nutrient-rich habitats (**section 3.3.3.1**). For example, in reef ecosystems, alien faunal distributions are linked to the presence of heavy metals, local population density and proximity to city ports; with invasive alien species being more common in areas with higher levels of pollution, while native species are less common under these conditions (Stuart-Smith *et al.*, 2015). In mangrove ecosystems in Nigeria, pollution and urbanization create forest gaps that enhance biological invasions, for example of *Nypa fruticans* (nipa palm; Nwobi *et al.*, 2020).

Urban areas generate and disseminate many types of pollutants, including nitrogen. Alien species are generally more tolerant to nitrogen pollution than native species (**section 3.3.3.1**), and in nitrogen polluted freshwater ecosystems in Hawaii, native goby species have declined while alien species are increasing (Lisi *et al.*, 2018). Urbanization generates runoff to aquatic ecosystems, which can carry many pollutants, and modifies their dynamics. An example is how pollution of freshwater environments following the application of road de-icing salts facilitates the survival and establishment of the invasive alien *Corbicula fluminea* (Asian clam) in New York, the United States, as this species is more tolerant to road salts than other native freshwater organisms (Coldsnow & Relyea, 2018).

Pollution can act directly by conferring advantages to more tolerant invasive alien species, but also by creating a competitive advantage for them by negatively affecting native populations. Human settlements generate domestic wastewater, agricultural fertilizer runoff, and effluents enriched with organic nutrients that, in coastal urban areas, often end up directly in the sea. In South Africa, these inputs of organic pollutants are associated with the bloom of *Ulva lactuca* (green laver) in Saldanha Bay (Mead *et al.*, 2013, **section 3.3.3.1**). In the Mediterranean Sea, high levels of urbanization are also linked with the degradation of coralligenous assemblages, compared to sites within natural protected areas and areas with lower rates of urbanization. This difference is, at least partially, associated with the increase of opportunistic alien species (e.g., algal species), which are more tolerant to urban-related pollution (Montefalcone *et al.*, 2017). In South East Australia, the heavily urbanized Port Jackson Estuary is one of the world's waterways most polluted by heavy metals and organic compounds as a result of antifouling paint, and this threatens the native *Saccostrea glomerata* (Sydney rock oyster), giving the more tolerant invasive alien *Magallana gigas* (Pacific oyster) a competitive advantage, and the invasive oyster, which also takes advantage of artificial substrates to establish has become more abundant (Scanes *et al.*, 2016). In coastal urbanized areas, copper, which is one of the primary active ingredients in antifouling hull paints, has become a common pollutant that increases in concentration as vessel traffic increases. A study carried out in Massachusetts proved that the invasive alien *Botrylloides violaceus* (violet tunicate) poses a competitive threat to the native *Aplidium glabrum* (tunicate) with regard to surface area growth when copper pollution is present. *Botrylloides violaceus* proved to be more tolerant to copper pollution (Osborne & Poynton, 2019). In Tasmania, expanding urbanization close to estuaries has resulted in an increase in pollutants from anthropogenic sources (e.g., marinas, storm-water drains, sewage outfalls and fish farms) that affect nearby benthic assemblages. Alien species were more abundant in sites near marinas and sewage outfalls (Fowles *et al.*, 2018). Increased focus on controlling pollution from marinas and sewage outfalls may thus limit the spread of alien species (Fowles *et al.*, 2018). In Lane Cove Valley, Australia, invasive alien plants are linked to areas polluted by phosphorus and heavy metals, which are pollutants linked with urbanization, and especially to areas where soil has also been previously disturbed (S. J. Riley & Banks, 1996).

Plastics are also a common waste product in urban areas, and exposure to plastics can change the behaviours of species. In Chile, Pinochet *et al.* (2020) studied invasive alien bryozoan species, such as *Bugulina flabellata* and *Bugula neritina* (brown bryozoan), that are frequently found in urbanized areas globally. These species tend to prefer plastic substrates, rather than wood or concrete, and exposure to plastic substrates could enhance their spread (**section 3.3.3.4**).

Finally, there are other types of pollution less frequently studied that are also linked to urbanization such as noise and light pollution. There are a few studies that assess the link between noise and light pollution in urban areas and invasive alien species. For example, the invasive alien *Hemidactylus frenatus* (common house gecko) in north-eastern Australia occupies a broader range of light environments than does the native gecko *Gehyra dubia* (dubious dtella). Experimental removal of the invasive alien gecko from places with light pollution, did not change the selection by native geckos for darker locations, which suggests cities are opening niches for invasive alien species (Zozaya *et al.*, 2015).

3.6 SYNTHESIS AND CONCLUSION

3.6.1 Literature used in this chapter and identification of knowledge gaps

A diverse strategy was adopted to identify and summarize the literature used in Chapter 3 (**sections 3.1.3** and **3.1.4**).[9] The varying approaches to reviewing the literature not only recognized the biases and gaps within the scientific literature linking invasive alien species with other drivers of change in nature (Hulme, 2022; **Box 3.13**), but also acknowledged the complexities in establishing cause-effect relationships between drivers and the transport, introduction, establishment and spread of invasive alien species (**sections 3.1.2** and **3.1.4**, **3.1.5**). Based on these search strategies, Chapter 3 summarizes the information from 1,183 scientific papers and other sources9 across indirect, direct, and other drivers of change in nature for the role of a total of 44 drivers in facilitating the transport, introduction, establishment and spread of invasive alien species across biomes, realms and IPBES regions (**sections 3.2** and **3.3**, **3.4**, **3.5**). Sections 3.2, 3.3, 3.4, 3.5 and 3.6.2 appraise and summarize the current state of knowledge on the role of drivers in facilitating biological invasions, whereas sections 3.1 and 3.6.1 outline the background and search strategies and summarize the knowledge base for the chapter.

Across the 1,183 studies identified and used in this report **(Figure 3.29)**:

- 30.4 per cent reported on indirect drivers of change in nature (sociocultural 2.2 per cent, demographic 9.5 per cent, economic 10.4 per cent, technology 5.9 per cent, governance 2.4 per cent);
- 72.1 per cent on linked to direct drivers of change in nature (land- and sea-use change 29.3 per cent, direct exploitation of natural resources 7 per cent, pollution 12.1 per cent, climate change 17.2 per cent, invasive alien species 6.5 per cent);
- 5.8 per cent on linked to other drivers (biodiversity loss 3.9 per cent, natural drivers 1.9 per cent).

Despite targeted searches to address how two or more drivers of change in nature interact to facilitate biological invasions (**sections 3.1.5**, **3.5**) fewer than 20 per cent of these studies reported on the role of more than one driver in facilitating biological invasions (**Boxes 3.12** and **3.13**).

9. Data management report available at: https://doi.org/10.5281/zenodo.5529309

Most studies were on invasive alien plants (52.8 per cent), which represents almost twice as many as for invasive alien vertebrates (28.9 per cent) or invertebrates (29.2 per cent), with fewer studies having been conducted on invasive alien microbes and fungi (12.3 per cent). More than half of the identified studies were from the terrestrial realm (66.3 per cent), whereas freshwater and marine systems were represented by, respectively, 20.2 per cent and 23.7 per cent of the studies. Plants dominated studies of terrestrial invasive alien species, whereas all macroscopic taxonomic groups were relatively evenly represented in the studies reviewed from the aquatic realms, with vertebrate studies being most numerous in the freshwater realm and invertebrate studies most numerous in the marine realm **(Figure 3.30A)**.

Reviewed studies mostly focused on drivers in the Americas (45 per cent), followed by Europe and Central Asia (36.6 per cent), with fewer studies from the Asia-Pacific region (34.5 per cent, noting that 23.2 per cent were from Oceania) and Africa (26 per cent). This trend was relatively consistent across all taxonomic groups **(Figure 3.30B)**.

For the majority of the studies analyzed in this report (1044 sources), it was possible to link drivers to one or more stages of the biological invasion process, with the majority of studies linking drivers to the establishment (70.5 per cent), spread (66.4 per cent) and introduction (53.5 per cent) of invasive alien species, whereas fewer sources explicitly linked drivers to transport (33.8 per cent). These numbers add up to considerably more than 100 percent, illustrating that most studies link drivers to more than one stage within the biological invasion process. The availability of studies on drivers varied across stages of the biological invasion process. Studies of the role of indirect drivers of change in nature in facilitating biological invasions tended to focus on links to transport and introduction of invasive alien species **(Figure 3.31A)**. This trend was especially evident for sociocultural and economic drivers, for which studies on their role in transport and introduction made up for two thirds (65 per cent) of studies on these two drivers across all stages of the biological invasion process. This pattern was consistent across all realms and taxonomic groups but is especially strong for microbes. In contrast, studies of direct (anthropogenic and other) drivers, reported

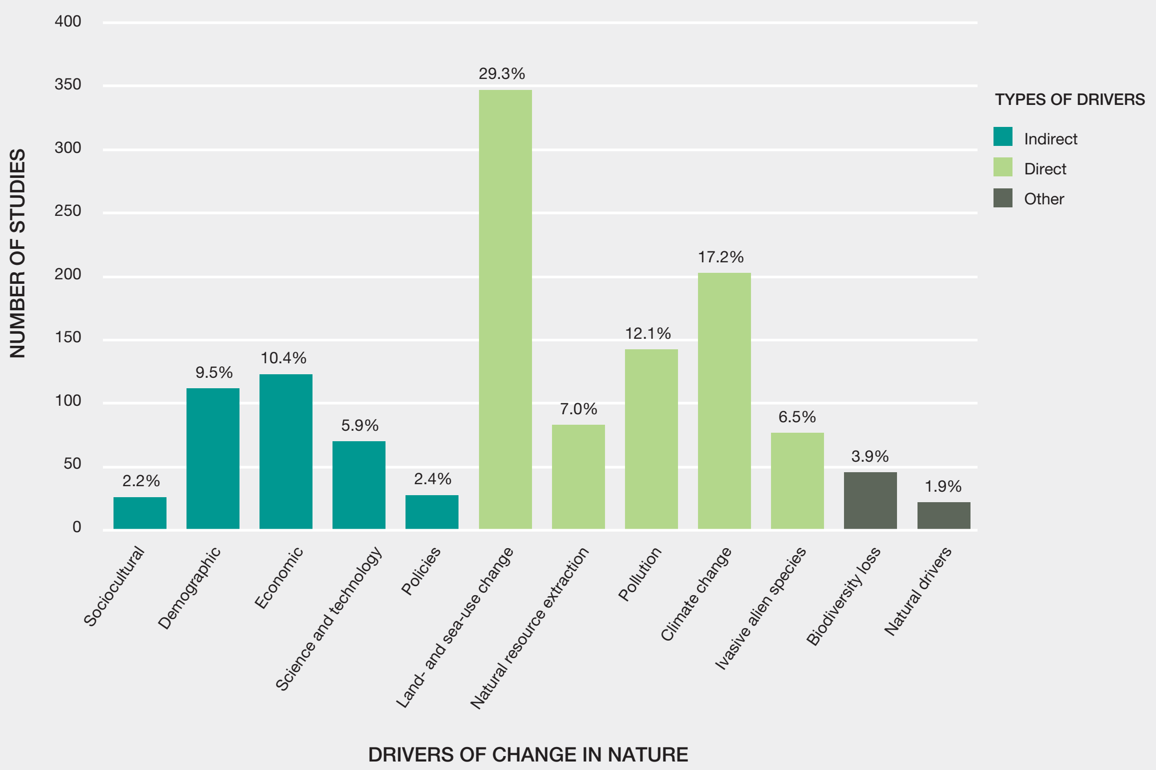


Figure 3 29 **Overview of the literature used for this assessment of the drivers of change in nature affecting biological invasions.**

The number of studies (y axis) in the literature base for Chapter 3 reporting on each driver of change in nature (x axis) in affecting biological invasions. The total number of studies is 1185. The underlying data for this figure is available at https://doi.org/10.5281/zenodo.5529309

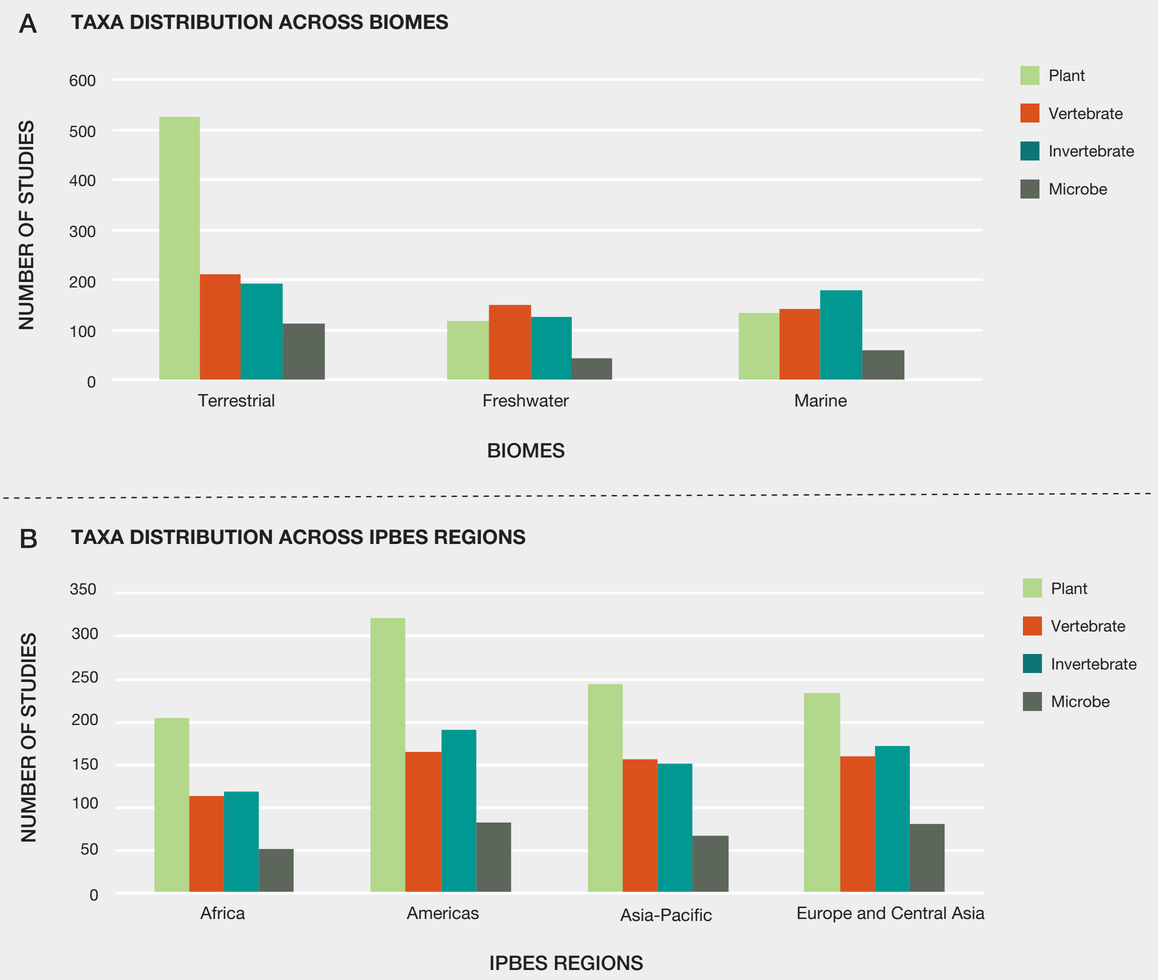


Figure 3 30 **Overview over the literature used for this assessment of the role of drivers of change in nature in affecting biological invasions across realms, IPBES regions and taxa.**

The number of studies in the literature base for Chapter 3 (y axis) reporting on the role of drivers of change in nature in facilitating invasive alien species categorized by realms vs. taxonomic groups (panel A.; x axis) and by IPBES regions vs. taxonomic groups (panel B.; x axis) (n = 1202 papers).The underlying data for this figure is available at https://doi.org/10.5281/zenodo.5529309

predominantly on links to the establishment and spread stages, a pattern that was especially evident for pollution, climate change, invasive alien species, biodiversity loss and ecosystem resilience, and for natural drivers, for all of which studies on their role in establishment and spread made up more than 75.9 per cent of all studies (**Figure 3.31B** and **C**). These patterns were less consistent across realms and taxonomic groups, however, as stronger links between direct or other drivers and establishment and spread were found in the terrestrial realm than in freshwater, whereas this pattern was largely absent in marine systems. Likewise, the link between indirect drivers and the early stages of biological invasion and direct drivers and later stages was strong for alien plants, but less evident for invertebrates and vertebrates, whereas studies of microbes predominantly reported on links to transport and introduction across all drivers. Three groups of drivers, demographic drivers, land- and sea-use change and direct exploitation of natural resources, stood out as studied in relation to all stages of the biological invasion process (**Figure 3.31A** and **B**). This was less evident for land-use and direct exploitation of natural resources in the terrestrial realm and for plants, where studies of establishment and spread dominate, and for demographic drivers for microbes, where studies of transport and introductions, dominated.

Information on the roles of drivers in facilitating biological invasions was largely sourced from primary studies (50.4 per cent), followed by reviews (40.9 per cent), whereas only a small number of studies were formal meta-analyses (3.6 per

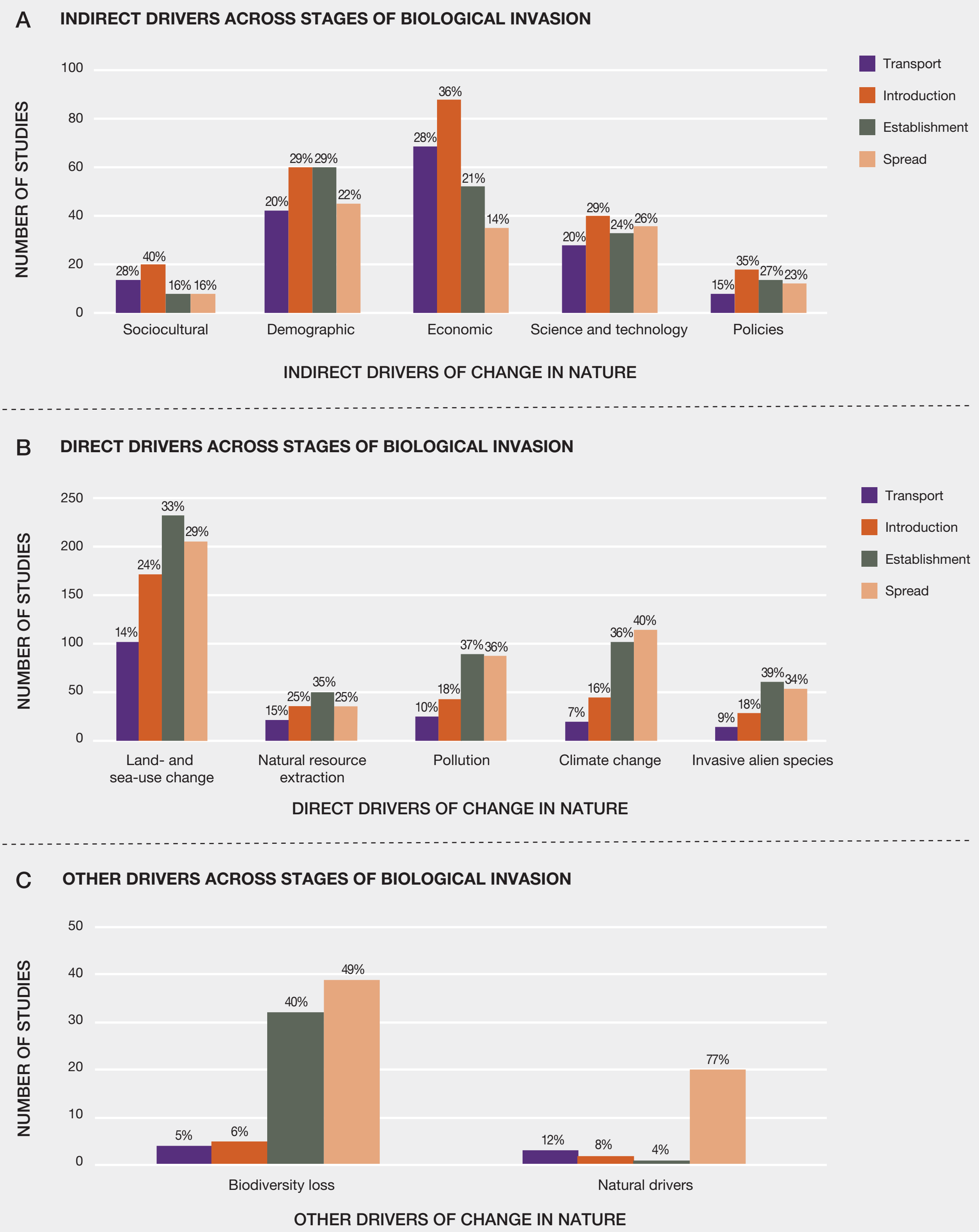


Figure 3 31 **Overview of the literature used within this chapter and specifically the role of drivers of change in nature in affecting invasive alien species across the biological invasion process.**

Summary of the literature extracted for Chapter 3 for assessing the role of drivers across biological invasion stages, showing the proportion of the studies of each driver that addresses the different stages in the biological invasion process. Note that studies used in the chapter that do not explicitly state stages of the biological invasion process affected are excluded from this figure, and that each study can address more than one stage of the biological invasion process (total of 1,183 papers). Chi-square analysis indicated

Figure 3 31

that the number of studies reporting effects on the transport and introduction of invasive alien species is statistically higher for indirect than direct drivers of change in nature (p<0,001), whereas the opposite is true for the establishment and spread stages. The number of studies is shown on the y axis, while the indirect (panel A.), direct (panel B.) and other drivers (panel C.) of change are shown on the x axis. For the number of studies for each driver, see **Figure 3.29**. The underlying data for this figure is available at: https://doi.org/10.5281/zenodo.5529309

cent). This suggests further structured synthesis and reviews are required to support the knowledge on the drivers facilitating biological invasions **(Box 3.13)**.

The outcomes of the chapter review with respect to data gaps and biases in the evidence available for assessing the role of drivers of change in nature in the context of biological invasions, are largely consistent with both the systematic review of scenarios and models[10] (**Chapter 1**, **section 1.6.7.3**) undertaken as part of this assessment **(Box 3.14)** and the bibliometric analysis of research effort undertaken by Hulme (2022) on drivers in relation to biological invasions **(Box 3.13)**.

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

Box 3 13 **Impacts of direct and indirect drivers of change in nature on biological invasions are currently much less understood than other areas of conservation science.**

A recent assessment of the research effort into the role of indirect and direct drivers of change in nature facilitating invasive alien species concluded that the current knowledge is limited, and focuses on tractable drivers over those that require an interdisciplinary approach, with bias towards developed economies (Hulme, 2022). Between 2000 and 2020, 27,462 peer-reviewed journal articles were published addressing biological invasions of which less than 5,000 (or 18 per cent) examined the role of one or more drivers of change in nature. In contrast, out of a corpus of 110,087 research papers targeting biodiversity and ecosystem services, almost 40,000 (or 36 per cent) described the role of one or more drivers. Thus, the drivers affecting biological invasions remain less understood compared to other areas of conservation science.

Research on drivers of change in nature facilitating biological invasions reflects a strong bias towards direct drivers with only a small fraction of studies addressing indirect drivers (Hulme, 2022). While there have been calls for increased interdisciplinarity in the study of biological invasions, the percentage of articles addressing indirect drivers of change in nature has shown no significant increase over the last two decades, leading to an increasing bias in articles towards direct drivers of change in nature (Hulme, 2022). Drivers deemed likely to be important for biological invasion by invasive alien species, such as governance and direct exploitation of natural resources, were shown to be poorly supported by research effort. The considerable literature addressing national and international policies for conserving biodiversity (Le Preste, 2017) is not matched by similar studies tackling the governance of problems arising from invasive alien species (Hulme, 2021a).

Compared to developed economies, there were only about half as many articles affiliated with institutions in developing economies. This may significantly limit the opportunity for prevention and projection of future risk of invasive alien species in Africa, Asia and Latin America. Given the future importance of indirect drivers such as tourism, trade and infrastructure projects on the likely risk of introducing invasive alien species to developing economies (Hulme, 2015a), the paucity of studies on indirect drivers is particularly troubling. Developing economies harbour most of the world's biodiversity (Adenle *et al.*, 2015) but also face significant threats from indirect drivers of change in nature such as international trade (Lenzen *et al.*, 2012) as well as direct drivers in the form of invasive alien species (Early *et al.*, 2016). Developing economies have also been identified as sources of many of the world's invasive alien species that have the potential to reach nearly all terrestrial biomes (Measey *et al.*, 2019). Thus, there is an imperative to improve the knowledge of drivers of change in nature in developing economies not only to protect their own national natural heritage but also prevent further biological invasions globally. The similarity between the results from the diverse literature review strategy in Chapter 3 and a systematic bibliometric analysis (Hulme, 2022) support the view that Chapter 3 adequately captures current knowledge of the drivers in facilitating invasive alien species.

Box 3 14 Representation of drivers in scenarios and models.[11]

Previous IPBES assessments have evaluated how various tools and techniques such as scenarios and models have been used to better understand the impacts of drivers on nature, nature's contributions to people and good quality of life (IPBES, 2016b, 2018e, 2018c, 2018d, 2019). For this assessment a systematic review was undertaken to evaluate the patterns and trends in published research on invasive alien species that included both scenarios and models (**Chapter 1**, **section 1.6.7.3**). In total 778 papers were reviewed (from an initial set of 30,299). Drivers were included as a scenario feature within the review with information captured on the number and type of driver. The results of the review showed that most papers focused on only one driver (77 per cent of 778 papers). Climate change was the most commonly included driver (62 per cent of all observations; **Figure 3.32**). The studies that focused on two or more drivers often included climate change or invasive alien species. Many of the drivers identified in **Chapter 3 (Table 3.1)** were poorly represented, as drivers such as demographics, governance, pollution, direct exploitation of natural resources, values and technology accounted for less than 2 per cent of the observations. The lack of studies focusing on interactions amongst drivers is a gap that could limit understanding of the outcomes of biological invasions alongside other drivers of change in nature.

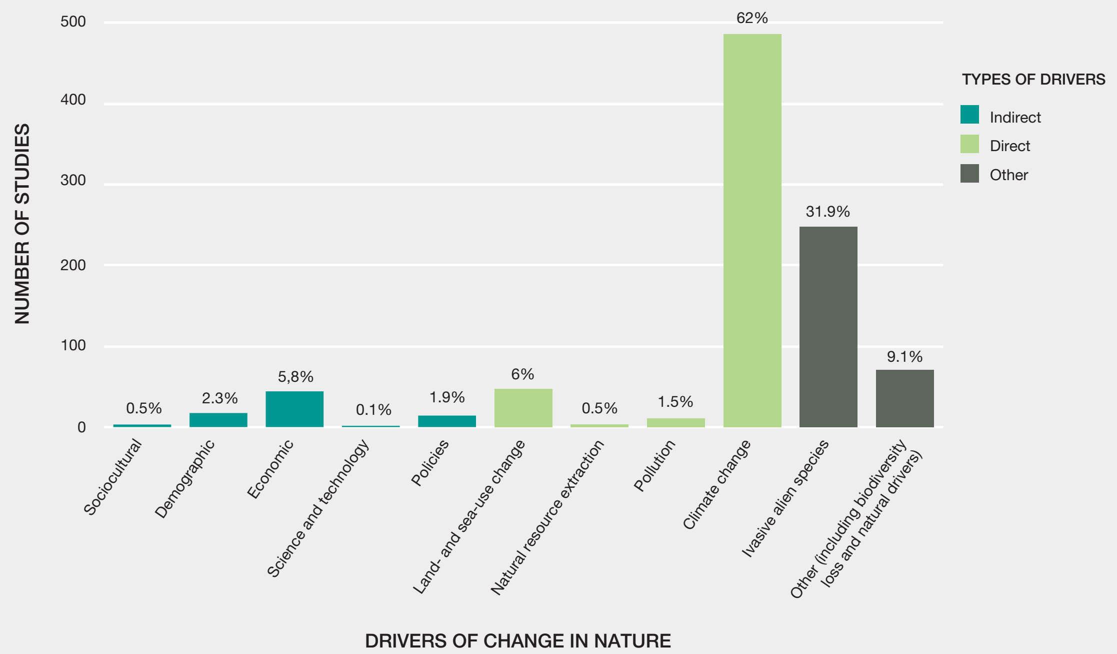


Figure 3 32 **Representation of drivers (per cent) of the observations for each driver across the papers included in the scenarios and models review noting some papers included multiple observations.**

The number of studies is shown on the y axis, and the different drivers of change in nature are shown on the x axis. A data management report for this figure is available at https://doi.org/10.5281/zenodo.5706520

The dominance of climate change as a driver in most studies is explained by the prevalence of correlative models which invariably include climate change scenarios (e.g., scenarios from the Intergovernmental Panel on Climate Change; IPCC) as a factor to project the occurrence or potential distribution of species. The majority of papers focused on exploratory scenarios, that examine a range of plausible futures based on the potential trajectory of key underlying scenario features. The results of these studies provide some insights in relation to future directions for the development of scenarios and models in invasion science (e.g., Lenzner *et al.*, 2019; Roura-Pascual *et al.*, 2021). Future studies may be able to address the current gaps and include the other cross-cutting themes highlighted in this assessment such as Indigenous and local knowledge (**Glossary**) and good quality of life (e.g., Obermeister, 2019), which would improve our understanding of the patterns and trends in drivers of change in nature and how these affect biological invasions.

11. Data management report available at https://doi.org/10.5281/zenodo.5706520

3.6.2 Synthesis

The relative importance of drivers of change in nature in facilitating biological invasions was quantified based on a consensus approach involving an expert-based assessment by the authors of the chapter for each invasion stage across and within realms (terrestrial, freshwater, marine) and broad taxonomic units (microbes, plants, invertebrates, vertebrates).[12]

Overall, the expert-based consensus approach assessed economic drivers as the most important in facilitating biological invasions worldwide (average 21 per cent importance, across all realms and taxonomic units, and stages of the invasion process), followed by land- and sea-use change (16 per cent), demographic drivers (10 per cent), climate change (9 per cent), sociocultural drivers and policies, governance and institutions (each 8 per cent), pollution (7 per cent), direct exploitation of natural resources and invasive alien species (each 5 per cent), biodiversity loss, natural hazards and science and technology (each 4 per cent). The major drivers identified are consistent with indigenous and local knowledge **(Box 3.15)**.

The consensus approach further reveals a clear shift in relative importance of the drivers over the stages of the biological invasion process **(Figure 3.34)**. The transport and introduction of invasive alien species are primarily facilitated by economic drivers, followed by land- and sea-use changes, with some evidence for an additional role of sociocultural drivers, demographic drivers, and policies, governance and institutions. In contrast, land- and sea-use change is the overriding driver responsible for the establishment and spread of invasive alien species, followed by climate change, pollution, and to some extent economic drivers and biodiversity loss. Thus, indirect drivers are identified as the most important in the early stages of the biological invasion process while direct drivers dominate in the later stages.

Patterns are relatively consistent across realms, but with some variation **(Figure 3.34A)**. Economic drivers and natural drivers are considered relatively more important and sociocultural and policy, governance and institutional drivers less important for facilitating the transport of invasive alien species in the marine realm, whereas demographic drivers are more important for the transport of invasive alien species into the terrestrial realm. There is little difference between realms in the relative importance of drivers facilitating the introduction stage. Policies, governance and institutional drivers are more important in facilitating the establishment of invasive alien species, while sociocultural drivers and biodiversity loss are less important in the marine realm, whereas demographic drivers are relatively more important and direct exploitation of natural resources less important in the terrestrial realm. Finally, the spread of invasive alien species is relatively less affected by demographic drivers in the marine realm, more affected by sociocultural drivers in freshwater systems, and less affected by pollution but more affected by biodiversity loss in the terrestrial realm.

There is more variation across taxonomic units than realms **(Figure 3.34B)**. Sociocultural drivers are consistently more important for facilitating alien plants early in the invasion process and for vertebrates across all stages, and less important for microbes and invertebrates. This pattern likely reflects the importance of intentional introductions of plants and animals for human amenity values, both linked to subsistence and to cultural values (**sections 3.2.1**, **3.2.3.2**, **3.2.3.3**, **3.3.1.1**). Demographic drivers are relatively more important for the transport of microbes than other taxonomic groups, whereas economic drivers are relatively less important for the introduction of plants and more important for the spread of plants and vertebrates than for the other taxonomic groups. This latter finding is likely linked to the relatively higher importance of land-use changes for the introduction of plants along with intentional introductions of alien vertebrates for hunting and farming (**sections 3.3.1.1**, **3.3.2.1.1**, **3.3.2.1.2**). Pollution is assessed as relatively more important for the introduction of microbes and less important for the establishment of invasive alien vertebrates and the spread of invasive alien invertebrates and vertebrates. In contrast, climate change is deemed relatively more important for the introduction, establishment and spread of microbes compared to other taxonomic groups.

These patterns illustrate some of the complexity in how drivers of change in nature facilitate biological invasions. The variation across stages, taxonomic units and realms is partly related to the biophysical characteristics of the specific processes and systems. As examples, trade and travel operate mainly through both the intentional and unintentional transport of invasive alien species across regions; harvesting and restocking for harvesting are more important in aquatic than terrestrial systems (**sections 3.2.3.1**, **3.3.2.1**) and respond to variation in human impacts (such as, land- and sea-use being more important for plants and pollution within aquatic systems and less important for vertebrates; **sections 3.3.1.1**, **3.3.3**).

12. Data management report available at https://doi.org/10.5281/zenodo.7861162

Box 3 15 Identification of drivers by Indigenous Peoples and local communities.[13]

The IPBES framework acknowledges diverse knowledge sources in assessments, and in particular the central position of Indigenous Peoples and local communities in providing situated understanding of biological invasions. Assessment authors thus carried out an extensive cross-chapter review of literature to identify Indigenous and local knowledge related to invasive alien species (**Chapter 1**, **section 1.6.7.1**). In total 131 studies were reviewed, and data on drivers was collated, including both the number and type of driver identified along with any comments or additional information.

In most cases, Indigenous Peoples and local communities identified at least one driver that had facilitated the invasion of the reported alien species (84 per cent of 131 papers). Land-use change was the most commonly included driver (identified in 40 per cent of all papers), but Indigenous Peoples and local communities generally judge indirect drivers of change in nature as relatively important in facilitating biological invasions, with economic drivers (32 per cent), policies, governance and institutions (24 per cent) and sociocultural drivers (21 per cent) as the three next-ranked drivers **(Figure 3.33)**. In the majority of studies (68 per cent), Indigenous Peoples and local communities identified more than one driver facilitating biological invasions, the average number of drivers being 2.25 (range 1-7). Of the studies, 72 per cent reported on the spread of invasive alien species, 18 per cent on their establishment, and 11 per cent on their introduction, with no studies reporting on the transport stage of the invasion process.

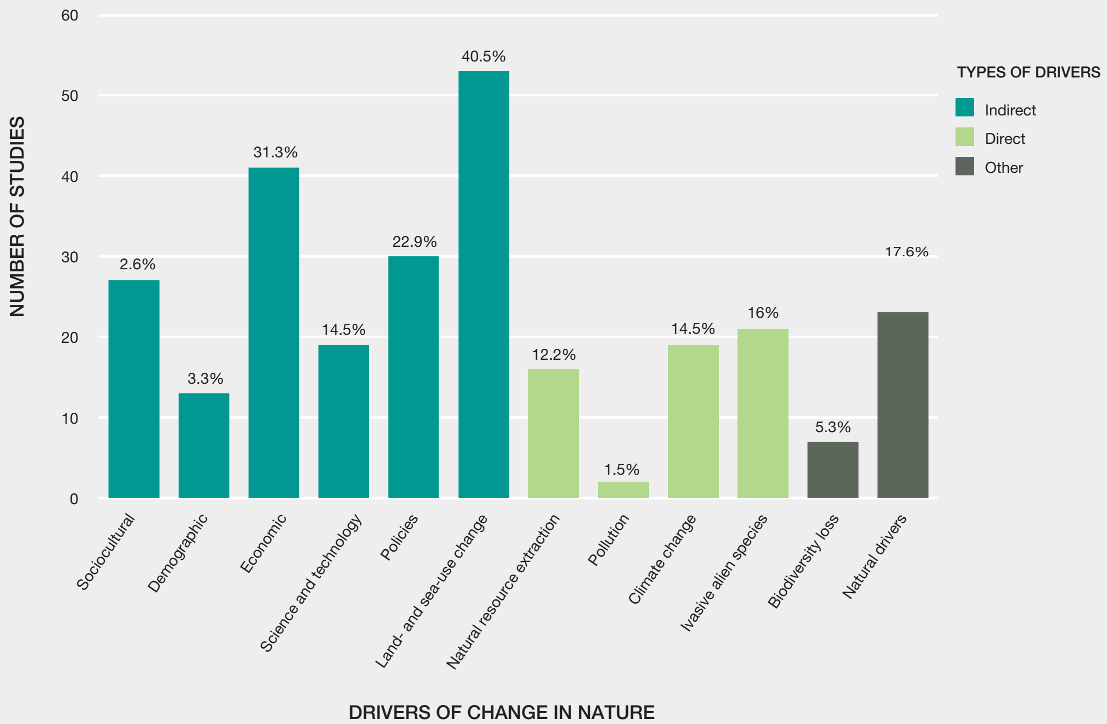
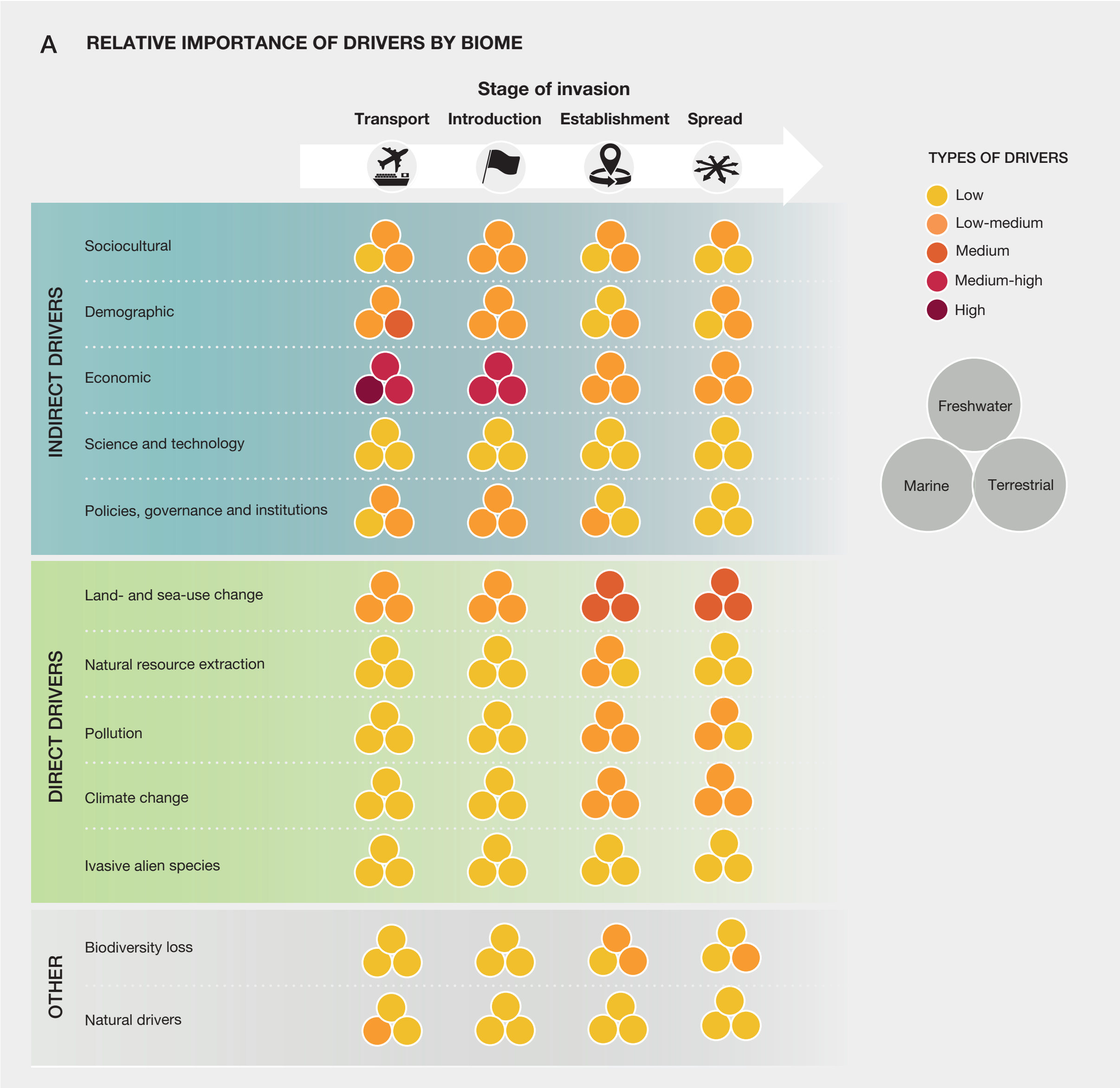


Figure 3 33 **Representation of the role of each driver in the studies included in the literature review on Indigenous Peoples and local communities and invasive alien species (numbers of reported cases across 131 references) in facilitating biological invasions, noting most papers included multiple cases.**

The number of studies is shown on the y axis, and the different drivers of change in nature are shown on the x axis. Data management report available at https://doi.org/10.5281/zenodo.5760266

13. Data management report available at https://doi.org/10.5281/zenodo.5760266


A RELATIVE IMPORTANCE OF DRIVERS BY BIOME
Stage of invasion
Transport
Introduction
Establishment
Spread
INDIRECT DRIVERS
Sociocultural
Demographic
Economic
Science and technology
Policies, governance and institutions
DIRECT DRIVERS
Land- and sea-use change
Natural resource extraction
Pollution
Climate change
Ivasive alien species
OTHER
Biodiversity loss
Natural drivers
TYPES OF DRIVERS
Low
Low-medium
Medium
Medium-high
High
Freshwater
Marine
Terrestrial

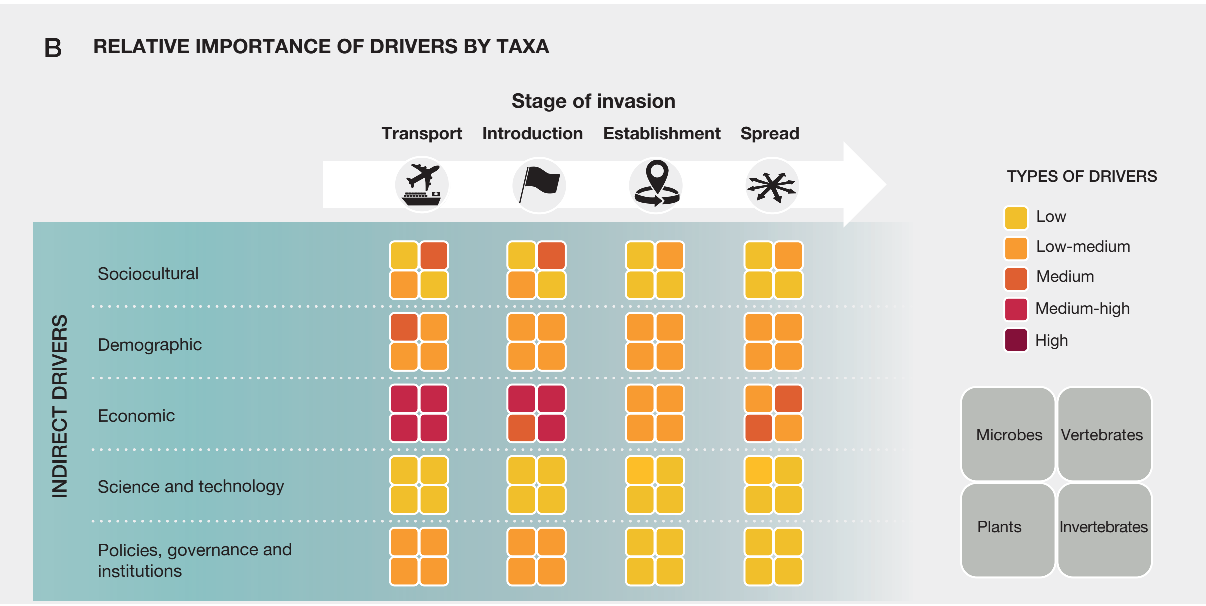

B RELATIVE IMPORTANCE OF DRIVERS BY TAXA
Stage of invasion
Transport
Introduction
Establishment
Spread
INDIRECT DRIVERS
Sociocultural
Demographic
Economic
Science and technology
Policies, governance and institutions
TYPES OF DRIVERS
Low
Low-medium
Medium
Medium-high
High
Microbes
Vertebrates
Plants
Invertebrates

Figure 3 34 **Assessment of the relative importance of indirect and direct drivers of change in nature in facilitating invasive alien species across stages of the biological invasion process, by A) biome (terrestrial, freshwater, marine) and B) taxa (microbes, plants, invertebrates, vertebrates).**

Separately for each realm and taxonomic unit, the Chapter 3 experts (coordinating lead and lead authors, fellows), scored the relative importance of each driver (out of 100 points) for each of the four stages of the invasion process. The scores of all panel members were then averaged to produce an overall consensus assessment, based on which the authors were allowed to adjust their individual scores (i.e., using a Delphi method approach). A data management report for this figure is available at https://doi.org/10.5281/zenodo.7861162

3.6.3 Conclusions

Indirect and direct drivers of change in nature play significant but varying roles across all four stages in the biological invasion process **(Figure 3.34)**. There is a clear shift from the early stages (transport and introduction), where indirect drivers of change in nature play overriding roles, and the later stages (establishment and spread), where direct drivers dominate. The transport and introduction of invasive alien species are primarily facilitated by economic drivers (**section 3.2.3**), in particular, international trade, primarily though maritime commerce, which has caused both intentional and unintentional transport and introduction of many invasive alien species in both terrestrial and aquatic realms, followed by land- and sea-use change (**section 3.3.1**), with other drivers playing smaller but still significant roles **(Figure 3.34)**. Land- and sea-use change is the overriding driver for the establishment and especially spread of invasive alien species, followed by climate change, pollution and to some extent demographic and economic drivers **(Figure 3.34)**.

There is variation in relative importance of drivers across realms and taxonomic groups, partly related to the biophysical characteristics of the specific systems (such as better connectivity in aquatic than terrestrial systems) and partially related to variation in human impacts. Sociocultural drivers are consistently more important for plants and vertebrates than for microbes and invertebrates across all stages of the invasion process **(Figure 3.34)**. This pattern probably reflects the importance of intentional introductions for human amenity value. Recent research on the role of drivers of change in nature in facilitating biological invasions has focused on the direct drivers, climate change and land-use change, whereas economic drivers are the most studied indirect driver. The importance of governance and sociocultural perspectives in shaping biological invasion remains understudied. Strong biases also occur in the biomes and taxonomic groups examined, with the majority of studies dealing with terrestrial temperate ecosystems relative to other biomes, and plants relative to other organismal groups (**section 3.6.1**). The evidence base for the role of direct and indirect drivers on invasive alien species is largely drawn from developed nations, particularly Europe, the United States and Canada as well as Australia and New Zealand. While most indirect and direct drivers of change in nature affect biological invasions across all regions and ecosystems, the magnitude of their effects will differ and the lack of detailed information for the Arctic and developing nations, especially sub-Saharan Africa, tropical Asia and South America, is of concern.

Intensification of drivers and the acceleration of biodiversity loss and ecosystem degradation will have consequences for biological invasions in the future. It is becoming clear that climate change will increasingly shape future trends in invasive alien species, potentially with a significant temporal lag (**Chapter 2**, **section 2.2.1**), and will modify the role that other direct and indirect drivers might play in facilitating biological invasions. Furthermore, ecosystems may become more vulnerable to biological invasions as invasive alien species themselves decrease biotic resistance to further biological invasions and/or biodiversity is lost (**sections 3.3.5**, **3.4.2**). All these concurrent changes in drivers and ecosystems are indicative that past patterns of biological invasions may not be effective in informing future invasion patterns. Of particular concern is the lack of understanding as to how different drivers of change in nature interact to affect biological invasions across the invasion stages.

Few drivers act in isolation (**sections 3.1.5**, **3.5**), and there are potentially many interactions among drivers that are likely to lead to future biological invasions scenarios never previously experienced. For example, international trade also influences other drivers of change in nature that facilitate biological invasions by intensifying urbanization around major trade ports, driving resource extraction to meet international market demands and increasing atmospheric and aquatic pollution (**section 3.5**). Similarly, land- and sea-use change has led to changes in disturbance regimes and habitat degradation, which can decrease biotic resistance to the establishment and spread of invasive alien species (**section 3.3.1**). Increasing and expanding trade, travel and urbanization are major drivers implicated in the introduction and spread of invasive alien species worldwide that at the same time facilitate ecosystem degradation, which in itself is a direct driver facilitating biological invasions (**section 3.1.2**). However, fewer than 5 per cent of published studies examining the role of drivers in facilitating biological invasion addressed more than one driver (**section 3.6.1**).

Intensification in many co-occurring drivers of change in nature in combination with interactive effects amongst drivers increase the risk of positive feedbacks exacerbating biological invasions in the future. Addressing these complexities can be achieved through interdisciplinary collaborations including scientists and policymakers. For example, future scenarios can be used to explore how economic, policy and demographic changes alongside and in response to climate change, land- and sea-use change, or pollution might lead to greater risk of biological invasions (i.e., the patterns described in **Chapter 2**). Such scenarios could then enable identification of the specific conditions, situations and combinations of drivers that are key in facilitating biological invasions, and that would therefore be critical to address in order to reduce threats and impacts from invasive alien species (**Chapter 4**). Only by investing in building these links between science and policy can risks of unintended policy outcomes, that lead to environmental degradation and biodiversity loss, be identified and avoided (**Chapters 5**, **6**). Better orientation and coordination of national and international research on drivers in relation to both their actual importance as well as their policy relevance in relation to biological invasions by invasive alien species is therefore key to addressing biological invasions in the future.

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