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This [invasion] velocity is proportional to the square root of the intensity of selective advantage and to the standard deviation of scattering in each generation.

(Fisher 1937)

1.1 Welcome to the Anthropocene

At the time of writing this book, we have witnessed an extreme case of biological invasion. A virus, through an evolutionary leap, has jumped onto a new host species, *Homo sapiens*, and has taken advantage of the new host's ambitions and mobility in the zealous phase of globalisation, causing a worldwide pandemic and economic meltdown. The 2019 coronavirus outbreak (COVID-19) is a showcase of the core of invasion science. A list of questions spring to mind. Why this particular virus, and not others? Why now? How fast can it spread? How is its spread mediated by climatic and other environmental factors? What are its vectors and pathways of transmission? Which regions and populations are most susceptible? How much damage can it cause to public health and economies? What factors cause substantial variation in mortality between human populations in different countries? How can we control it? Can we forecast and prevent future outbreaks of emerging infectious diseases? While the whole world scrambles to make sense of COVID-19 and to combat the biggest crisis for humanity since World War II (WWII), we embark on a journey to address these questions to cover many more taxa and situations – the invasion of any biological organism into novel environments.

All species have the means to shift their progeny, either via direct movement or through vector-mediated dispersal. The incentive to move has driven Earth's biota to cover all possible niches, from the Antarctic to the Arctic, from the Himalayas to the Mariana Trench. Most propagules,

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however, move slowly and over short distances. On very rare occasions do propagules catch a ride on ocean rafts or hurricanes, or become attached to a seabird. Such propensity and limitation of dispersal are key factors behind the world's distinct biotic zones. This process of natural dispersal and spread of species was altered by early hominids. Hunter-gatherer societies had deep knowledge of the animals and plants around them and started to cultivate many species to ensure a sustainable supply of food and fibre. When humans began colonising the entire planet, cultivated plants and animals moved with them, the result being a growing list of species able to thrive in human-dominated environments, with the capacity to transform landscapes. Not only did humans intentionally move many species with them to supply their needs, but their movements also resulted in the accidental movement of many species. These include species associated with useful organisms, such as yeasts, viruses and other microorganisms, and many other types of pest and weed that simply 'hitched a ride' on diverse means of transport. Human selection has resulted in a rather unique assemblage of species, distinct from those that occur in natural communities and which are filtered by natural selection.

Human-mediated movement of species has accelerated dramatically in the era of globalisation, in terms of quantity, distance and speed. Technological innovations have revolutionised ways in which we transport goods. Stretching from Xi'an to Rome, the Silk Road connected the Eurasian supercontinent as early as the first century BC, carrying goods on the backs of horses and camels. Islamic merchants created the Spice Route in the seventh century, thereby connecting the Mediterranean Sea and the Indian Ocean. Global trade started in earnest in the Age of Discovery, when European explorers connected East and West with the Americas in the fifteenth century. Global trade scaled up after the first Industrial Revolution in the eighteenth and nineteenth centuries when global production chains began compartmentalising (e.g. meat export from South America). The trajectory has been interrupted only by two World Wars and the COVID-19 pandemic. After WWII, globalisation resumed its march with the mainstream transport of cars, ships and planes (global export totalling US\$62 billion in 1950), only being slowed temporarily by the Iron Curtain during the Cold War. A milestone of this globalisation was the launch of the World Trade Organisation in 1995, when global exports reached US\$5 trillion. Globalisation then soared over the next two decades, with bumps along the way during the 2008 recession and the COVID-19 pandemic,

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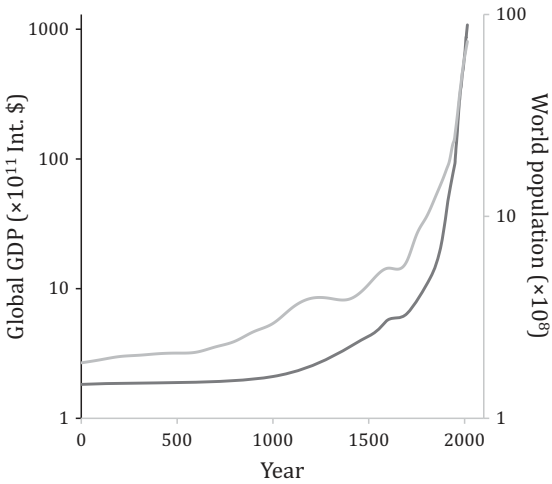


Figure 1.1 Global GDP, in international dollars (2011 price), and world population, in the past two millennia. Based on data from ourworldindata.org under CC-BY Licence.

reaching close to US\$19 trillion in 2014. Real gross domestic product (GDP) per capita in the United States in 2014 was four times the size it was in 1950. The human population increased from 2.5 billion in 1950 to 7 billion in 2012 (Figure 1.1), and is projected to reach 10 billion in 2050. Not only has our ecological footprint overshoot the planet's carrying capacity, but there are also emerging global crises that are threatening the whole of humanity (e.g. climate change, biodiversity loss and the pandemic).

With the rising dominance of humans in the biosphere, previously characteristic floras and faunas in regional biotic zones have been mixed and reshuffled, resulting in a major homogenisation of the world's biota. The accumulation of non-native species across the globe is continuing with no sign of a slowing of the rate of new records of naturalisation and invasion (Seebens et al. 2017). Putting aside biases in taxonomy and sampling effort, the trend in the global rate of new records of established non-native species is overwhelming (Figure 1.2). Geographic and taxonomic variations in the dynamics and rate of non-native establishment reflect the role and history of regional countries in global trade. With the rise of global trade, the rate of establishment of non-native species has increased steadily, as stowaways, contaminants and pets since 1800, and

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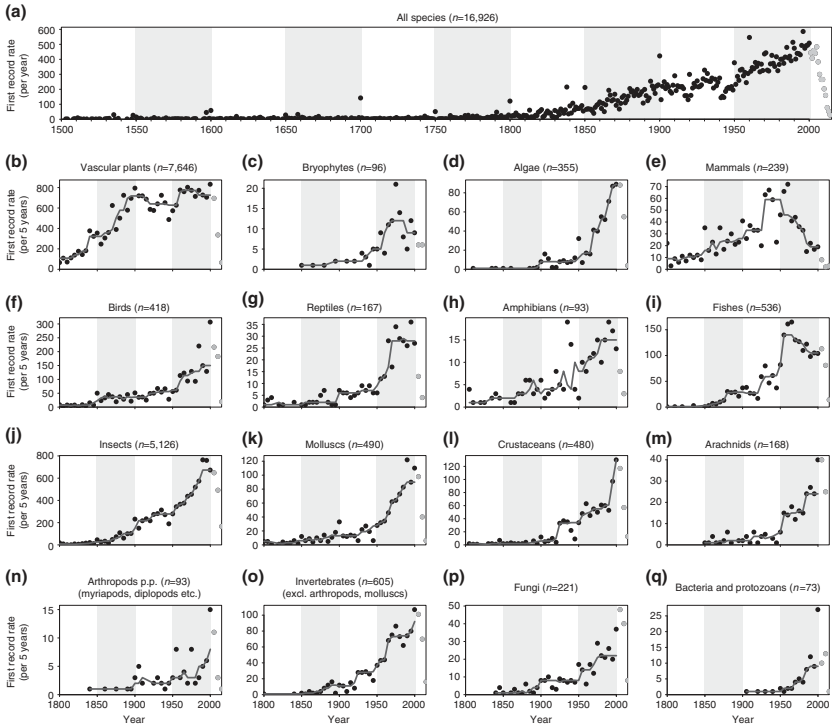


Figure 1.2 Global temporal trends in the rates of first records of the establishment of non-native species. Global temporal trends in first record rates (dots) for all species (a) and taxonomic groups (b–q) with the total number of established non-native species during the respective time periods given in parentheses. Data after 2000 (grey dots) are incomplete because of the delay between sampling and publication, and therefore not included in the analysis. As first record rates were recorded on a regional scale, species may be included multiple times in one plot. (a) First record rates are the number of first records per year during 1500–2014. (b–q) First record rates constitute the number of first records per 5 years during 1800–2014 for various taxonomic groups. The trend is indicated by a running median with a 25-year moving window (red line). For visualisation, 50-year periods are distinguished by white/grey shading. From Seebens et al. (2017) under CC-BY Licence.

accelerated further after 1950 – with the sole exception of mammals and fishes, which exhibit a hump-shaped curve, perhaps due to the regulations on farming for the game and fur industry. The establishment of non-native plant species has maintained a high rate since 1900 (Figure 1.2), coinciding with acclimatisation and colonisation activities in European diasporas. Technology has enabled us to move species around the world in new ways, quickly and in huge numbers; and

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changing fashions, fads and desires of human societies are continuously modifying and expanding the catalogue of translocated species – not just for essential goods but also for peculiar luxuries and hobbies. We need new ways of categorising and managing the new assemblages of biota that occur in different environments. Not only do we need to understand how many species are moved around the world by humans, but we also need to understand how these species interact with other species and how the added species and the changes that they bring affect the functioning of ecosystems, and thereby influence our well-being, both positively and negatively.

Biological invasions are by no means the only driver of the massive global-scale environmental changes that we are seeing. Invasive species interact in complex ways with other key builders and shapers of novel ecosystems such as agriculture, urbanisation, altered biogeochemical cycles, excessive carbon emission and pollution. For instance, of the documented 291 records of plant species extinction (Le Roux et al. 2019), agriculture, urbanisation, grazing, habitat degradation and destruction, together with biological invasions, are found to be implicated. The exact role of each of these factors is difficult to discern in most cases, but each surely has its own distinct temporal pattern and role to play (Figure 1.3). With these burgeoning factors affecting the planet's biosphere, we are witnessing pervasive alterations to physical systems, disturbance regimes and biogeochemical cycles, leading to a downward spiral in the integrity and health of ecosystems, accompanied by biodiversity loss and ecosystem transformation. In some cases, biological invasions are directly responsible for the decline of native biota, e.g. native plant species in Mediterranean-type ecosystems have been severely affected by non-native plants, particularly by Australian acacias (Figure 1.4; Gaertner et al. 2009). Recent reviews on the role of biological invasions in reducing the biodiversity of recipient ecosystems overwhelmingly support this view of the detrimental role of invasive species, more so at local than regional levels (Figure 1.5; Chase et al. 2018). These forces of change sometimes reinforce each other at different spatial and temporal scales, often with lags, leading to complex and intertwined challenges to the well-being of humanity and ecosystems (Díaz et al. 2015; Essl et al. 2015a). On this wagon of humanity, many hitchhiker species proliferate, creating harmful impacts on human well-being. The huge number of species that have been transported by us in different quantities and rates, intentionally or not, directly or not, define the subject and context of invasion science (Pyšek et al. 2020a).

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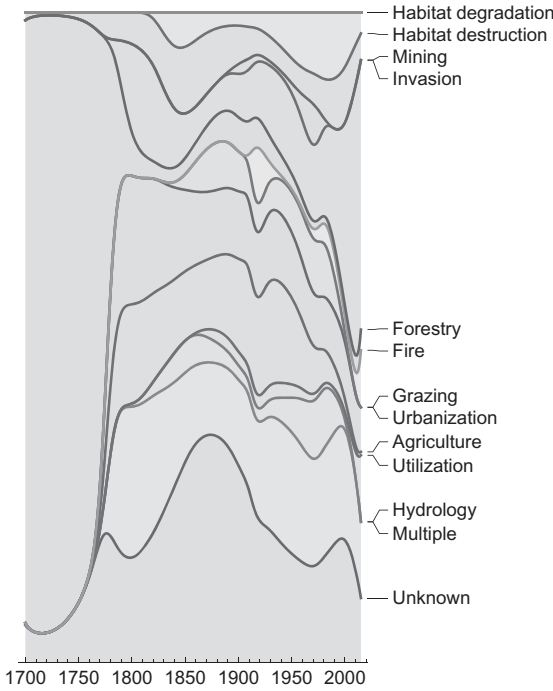


Figure 1.3 Primary drivers of plant extinctions over the last 300 years shown as area graphs to visualise the temporal changes in the relative contribution of the 11 identified primary extinction causes. Data from Le Roux et al. (2019).

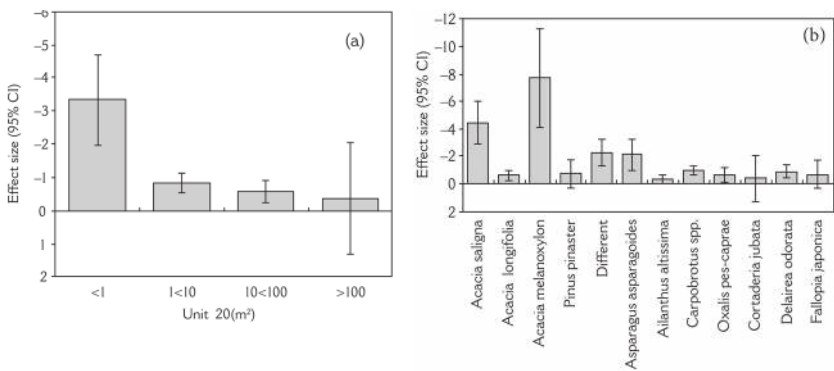


Figure 1.4 Effect size (95% CI) of invasion on species richness for different (a) unit sizes and (b) taxonomical groups in Mediterranean-type ecosystems. Q-test shows significant different effect sizes (heterogeneity) between unit sizes and between species. From Gaertner et al. (2009), reproduced with permission.

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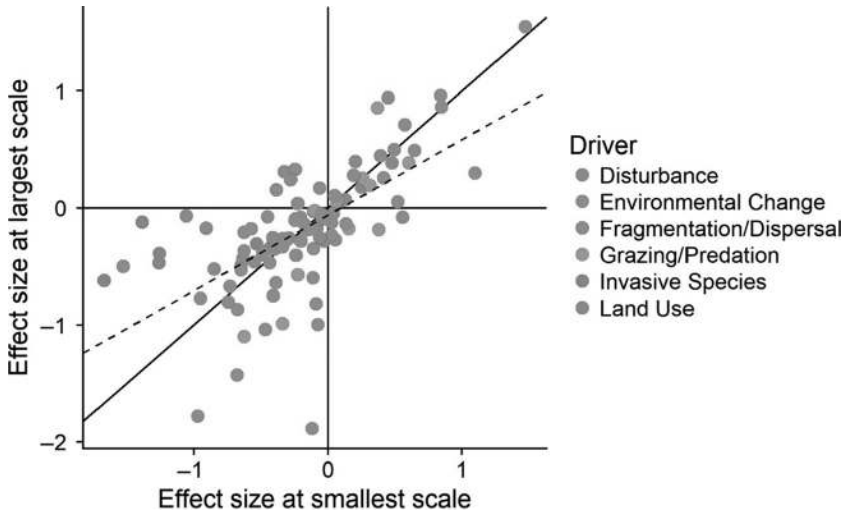


Figure 1.5 Results of a meta-analysis of scale-dependent responses to a number of different ecological drivers. Points represent the log response ratio comparing species richness in control to treatments in a given comparison measured at the smallest (x-value) and largest (y-value) scale. The solid line indicates the 1:1 line expected if effect sizes were not scale dependent. Points above and below this line indicate effect sizes that are larger or smaller, respectively, as scale increases; points in the upper left and lower right quadrants represent cases where the direction of change shifted from positive to negative, or vice versa, with increasing scale. The dashed line indicates the best fit correlation, which is significantly different than the 1:1 line ($P < 0.01$), indicating that overall, effect sizes tend to be larger at smaller scales than at larger scales. Colours for points indicate categorisations into different ecological drivers. From Chase et al. (2018), reproduced with permission.

1.2 The Making of a Discipline

Although the human-mediated translocation of species has been documented anecdotally since antiquity, the concept of biological invasions is a very recent construct. Many naturalists in the 1800s wrote of non-native species, but it was only in the mid-1900s that the scale of human-mediated movements of species and the growing importance of the implications of such movement became apparent. Pioneers of ecology in the nineteenth century – among them Charles Darwin, Augustin and his son Alphonse de Candolle, Joseph Dalton Hooker and Charles Lyell – explored the role and performance of a small number of non-native species in competition with indigenous ones. Lyell (1832) wrote,

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every species which has spread itself from a small point over a wide area, must, in like manner, have marked its progress by the diminution, or entire extirpation, of some other, and must maintain its ground by a successful struggle against the encroachments of other plants and animals.

Such appreciation of invasive spread leading to species extinctions predates the rise of global change biology in the late twentieth century (Wilkinson 2002). When writing about the European thistle cardoon, *Cynara cardunculus*, in his journal of research into the geology and natural history of the various countries visited by HMS *Beagle*, Darwin (1839) commented,

I doubt whether any case is on record, of an invasion on so grand a scale of one plant over the aborigines [of South America].

Following these early accounts of non-native species, many ecologists in the early twentieth century began synthesising the scattered knowledge of the ecology of non-natives, unknowingly taking the first tentative steps towards creating a framework for conceptualising biological invasions. Albert Thellung, in his 1912 Habilitation thesis *La Flore Adventice de Montpellier*, offered an early population-based definition of naturalisation which implied the notion of penetration of environmental barriers. He also devised concepts to classify the non-native flora of Montpellier in France according to their degree of naturalisation, introduction pathways and residence time (Kowarik and Pyšek 2012). Unfortunately, such work did not have much, if any, influence on the emerging field of ecology, and the ideas were only rediscovered in the late twentieth century, as the underpinning concepts of invasion science began coming under intense scrutiny.

Charles Elton's (1958) classic book *The Ecology of Invasions by Animals and Plants* is recognised as a milestone in the development of the field now known as invasion science (Richardson and Pyšek 2007, 2008). Already expressed in Elton's (1927) book on *Animal Ecology*, the Eltonian niche is an important concept for formulating a species' position in an ecological network using its functional traits, as will be elaborated in later chapters. Following this line of thinking, Elton (1958) speculated that island assemblages are filtered for a small portion of colonisers, which subsequently cannot fully explore the island's resources and are therefore more susceptible to invasions than those on the mainland. However, the publication of Elton's book was not immediately followed by a significant rallying of research effort. Unlike some other books on

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environmental topics, Elton's book on invasions had a negligible impact on public perceptions and launched no major actions (Hobbs and Richardson 2010). At about the same time as Elton's book appeared, geneticists began synthesising concepts pertaining to the evolution and genetics of colonising species (Baker and Stebbins 1965). These insights provided crucial stepping stones to the development of the central tenets of invasion science, including the determinants of invasion success, life-history trade-offs, generalist versus specialist strategies, general-purpose genotypes, adaptive phenotypic plasticity, mating systems and the influence of bottlenecks on genetic variation (Barrett 2015). Perhaps the most important linkage of Elton's (1958) classic volume to the theme of our book is his notion that decreased diversity leads to decreased stability. This complexity–stability relationship has stimulated long-lasting debates in ecology with substantial inputs from many figures in the field, including Robert MacArthur, Robert May and G. Evelyn Hutchinson. As will be shown in Chapter 4, ecological networks facing biological invasions typically violate this relationship but simultaneously reveal their trajectory of transition and turnover.

In 1980, the third international conference on mediterranean-type ecosystems, termed MEDECOS, was held in Stellenbosch, South Africa. The invasion of fynbos vegetation by non-native trees, a prominent topic of discussion at this meeting, conflicted with the dominant view of the time, which was that human-induced disturbance was the prerequisite for invasion into pristine ecosystems. A proposal drafted at the Stellenbosch meeting led to an international programme on the ecology of biological invasions under the auspices of the Scientific Committee on Problems of the Environment (SCOPE) (Mooney 1998). Its first five-year plan (1982–1986) revisited Elton's key assumptions and generalisations, reviewed the status of invasions worldwide and addressed three key questions relating to invasiveness, invasibility and management. The SCOPE programme attracted some of the world's top ecologists and comprised national, regional and thematic groups covering all aspects of invasions (Drake et al. 1989). Through the SCOPE programme, invasion science has firmly established itself as an exciting and relevant research field within global change biology (Simberloff 2011). In 1996, an influential conference in Trondheim, Norway, concluded that invasions had become one of the most significant threats to global biodiversity and called for a global strategy to address the problem (Mooney 1999; Sandlund et al. 1999). This led to the launch of the Global Invasive Species Programme (GISP Phase 1) in 1997, with more

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transdisciplinary goals than the SCOPE programme, acknowledging the need for work on economic valuation, stakeholder participation and pathway analysis and management (Mooney et al. 2005). The Convention on Biological Diversity (CBD), Article 8(h), calls on member governments to control, eradicate or prevent the introduction of those non-native species that threaten ecosystems, habitats or species. In 2000, the IUCN published their guidelines for the prevention of biodiversity loss caused by non-native invasive species. The 1990s saw the blossoming of invasion science, with the number of publications growing rapidly in all related fields (Vaz et al. 2017). In 2018 the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services (IPBES) launched a thematic assessment of invasive non-native species and their control.

Invasion science, as is the case with any emerging discipline, has exhibited different phases. From 1950 to 1990, studies on biological invasions were rather sparse, with fewer than ten publications per year according to the ISI Web of Science. In 1999, the journal *Biological Invasions* was launched, with its founding editor James T. Carlton (1999) stating,

[the aim of] *Biological Invasions* [the journal] . . . is to seek the threads that bind for an evolutionary and ecological understanding of invasions across terrestrial, fresh water, and salt water environments. Specifically, we [the journal] offer a portal for research on the patterns and processes of invasions across the broadest menu: the ecological consequences of invasions as they are deduced by experimentation, the factors that influence transport, inoculation, establishment, and persistence of non-native species, the mechanisms that control the abundance and distribution of invasions, and the genetic consequences of invasions.

The period 1990 to 2010 saw the rapid rise of invasion science and its multidisciplinary tentacles (Richardson et al. 2011; Vaz et al. 2017). During this phase, competing concepts, hypotheses, models and knowledge frameworks have been proposed and debated, and consensus has been reached on many fronts; we call this ‘Invasion Science 1.0’. Knowledge systems developed during this period accumulated mainly through individual case studies and comparative studies, with the focus being on the invader itself. Developments in the study of invasions at this time must be considered within the context of the intellectual landscape of the day. Indeed, following the Clements–Gleason debate, the Gleasonian individualistic notion that species function independently from the influence of others was implicitly accepted by most researchers as the foundation on which to build frameworks and concepts about