





Review

Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide

Philip E. Hulme^{1,*}

¹The Bio-Protection Research Centre, Lincoln University, PO Box 85084, Christchurch 7648, Canterbury, New Zealand *Correspondence: philip.hulme@lincoln.ac.nz

https://doi.org/10.1016/j.oneear.2021.04.015

SUMMARY

Biological invasions are synonymous with international trade. 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. But trade also has an indirect role on biological invasions by transforming the environments and societies of exporting and importing nations. Here, both the direct and indirect roles of trade on biological invasions, as well as their interaction, are examined for the first time. Future trends in international trade, including e-commerce, new trade routes, and major infrastructure developments, will lead to the pressure on national borders soon outstripping the resources available for intervention. The current legislative and scientific tools targeting biological invasions are insufficient to deal with this growing threat and require a new mindset that focuses on curbing the pandemic risk posed by alien species.

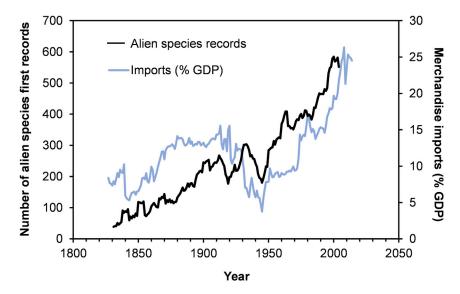
INTRODUCTION

Alien species are defined as those taxa whose presence in a region is attributable to human transport, whether deliberate or accidental, that has enabled them to overcome fundamental biogeographical barriers to their geographic distribution. ^{1,2} For millennia, as humans have moved across the globe as permanent migrants, short-term tourists or even with invading armies, alien species have hitched a ride on clothing and livestock, in personal goods and food, and even as companion animals or plants.^{3,4} Yet, despite the importance of human travel and migration to the introduction and establishment of alien species in new regions, international trade is widely regarded as the primary driver of biological invasions in both terrestrial and aquatic ecosystems. 5-8 International trade occurs as a result of geographical specialization, whether in terms of the availability of natural resources (e.g., Brazil nuts, minerals, marine fisheries) or in the production of goods (e.g., kiwi fruit, iPads, vaccines), and consequently buyers and sellers reside in different countries. In some cases, the commodity traded may itself be an alien species (e.g., ornamental fish or plants) but often alien species are introduced unintentionally as a contaminant of traded commodities (e.g., weed seeds in grain, parasites in livestock) or as a stowaway on transport vessels or other means of conveyance (e.g., hull fouling biota on ships, soil on the exterior of cargo containers).9 Given the robust evidence that many invasive alien species have major negative impacts on human health, food security, ecosystem services, and biodiversity, understanding the role international trade plays in biological invasions is crucial to secure sustainable economic outcomes. 10

Although international trade has been a feature of human society for thousands of years, 11 since the beginning of the 19th century the share of the world Gross Domestic Product (GDP) accounted for by merchandise imports has more than tripled (Figure 1). The growth in volumes handled by international transportation, particularly by container shipping, has been especially marked since the 1990s due to the surge in global exports in the wake of rapid industrialization in developing economies and the massive offshoring of manufacturing, particularly in China. 12 The number of new occurrences of alien species recorded each year worldwide has outpaced the growth of international trade, increasing almost 20-fold since the start of the 19th century (Figure 1). The positive association between the first records of alien species and the percentage contribution international imports make to GDP is clearly evident, but is much stronger in recent decades (for 1950 to 2000, Pearson correlation r = 0.92, df 49, p < 0.00001) than before 1950 (for 1827 to 1949, Pearson correlation r = 0.31, df 121, p < 0.00053). Bilateral trade has grown dramatically since the 1950s with the numbers of reported countries and trading partners increasing over time from 76 countries and 5,700 country-country bilateral trade pairs in 1948 to 186 countries and 34,410 pairs in 2000.¹³ Governments engaged in international trade have a long history of implementing controls on the import and export of merchandise commodities, and national legislation has become increasingly shaped by international trade rules. 14 This trend is clearly illustrated in the growth of regional trade agreements that have come into force since 1950 and encourage the free movement of goods across the borders of signatories (Figure 2). A significant factor in the







development of national and international regulations has been the need to reduce the risk of introducing alien pests and diseases of agricultural significance through trade. 15 It would be expected that with the growth in international trade so the likelihood of alien species being introduced as commodities, contaminants, or stowaways will also increase. Not surprisingly, trends in international trade have often been used as the basis for projecting future risks of invasive alien species. 13,16-18

However, to date the interpretation of international trade as a driver of biological invasions has often been too simplistic. It is essential to consider the multidimensional nature of trade that not only includes the direct effects of changes in the trade network and volume of commodities transported but also the indirect effects through other social and physical drivers that may be equally, if not more, important. Both this complexity as well as significant emerging issues are explored in this review by examining the evidence of international trade as not only a direct driver, especially as a result of technological change that has accelerated rates of biological invasions, but also as an indirect driver stemming from the role international trade is playing in resource extraction, pollution, urbanization, and climate change that in themselves also facilitate invasions. The marked interactions between the direct and indirect roles of international trade on biological invasions are examined and shown to be highly dynamic such that past trends are not necessarily a sound basis to predict future prospects. One clear message is that more effective regulation of international trade is urgently needed to limit the risks of future biological invasions.

TECHNOLOGICAL INNOVATIONS IN TRADE FACILITATE INVASIONS

Despite invasive alien species being viewed as one of the most important contemporary drivers of biodiversity change worldwide, 10 humans have moved species through trade across biogeographical barriers for millennia. For example, a substantial influx of alien plant species to the UK occurred in the Late

Figure 1. Global trade and invasions over time

Temporal change since the early 19th century in the percentage of GDP comprising imports¹⁹ and the number of first records of alien species worldwide.²⁰ For clarity, data on first records of alien species are presented as 5-year running averages.

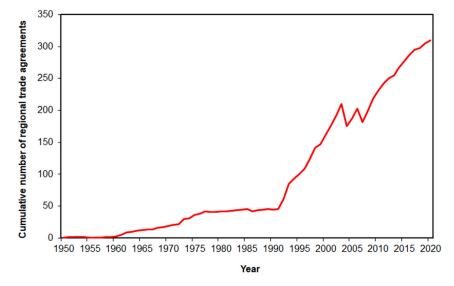
Bronze Age (1000-700 BC), possibly reflecting changes in agriculture and the increasing trade and transport at that time.21 Yet the role played in the spread of alien species by the extensive trade networks that criss-crossed Mesopotamia in the Early Bronze Age (3000 BC) and linked Europe, North Africa, the Middle East, and South Asia22 can only be conjectured. Undoubtedly, the movement of people, crops, and livestock prior to detailed floristic and faunistic records

has blurred the distinction between the native and introduced ranges of many species.

Although there is clear evidence that ancient introductions have been severely underestimated, there is no arguing with the evidence that the past two centuries have witnessed a dramatic increase in the number of alien species recorded worldwide.²⁰ International trade has been identified as one of the primary reasons for this increasing trend since the acceleration of global commerce coincides with the escalation in alien species numbers.²³ Reviews of the history of trade have shown that the dramatic gear shift in international trade since the 1800s was the product of technological change, infrastructure improvements, and a less protectionist global economy. 14,24 However, how these major technological and infrastructural developments have accelerated the opportunities for introducing alien species around the world has not been elaborated in detail. In this section, seven major technological developments that accelerated trade are shown to also be major drivers of alien species invasions: the increased speed of transport by sea, new trade routes, changes to ballast, the use of refrigeration, containerization, air transport, and the development of global communication technologies.

The introduction of the ocean-going steamship in the 1840s sharply reduced transport costs and ocean freight rates fell 70% between 1840 and 1910 because of technological change and improved navigation techniques.²⁵ Ship size increased from the largest tonnage of 3,800 gross registered tons (revenue-making cargo space) in 1871 to 47,000 tons in 1914. 12 Steamships took approximately half the time to cross the Atlantic as vessels that relied solely on sails and this meant that alien species were more likely to survive the journey and avoid detection. The introduction of the potato late blight fungus (Phytophthora infestans) from Mexico to Ireland in 1845 likely occurred because the shorter journey time on steamships meant that disease symptoms were less evident on the imported tubers and thus they were imported into the country, whereas previously the longer incubation times under sail would have resulted in infected consignments having rotted on board and thus being





rejected.²⁶ Today, the shorter travel times that link-up the world mean that surviving transport is much less of a barrier to the introduction of alien species than it was in the past.

Sailing ships still dominated the longer journey to Asia but this changed when the Suez Canal opened in 1869, halving the distance between London and Bombay and allowing steamships to carry more cargo and less fuel, effectively ending the commercial reign of sail.²⁴ Unfortunately, several hundred marine species in the western Indian Ocean and Red Sea have been subsequently able to traverse the Suez Canal and establish alien populations in the Mediterranean Sea with considerable negative consequences for native species.²⁷ In contrast, while the opening of the Panama Canal in 1914 also substantially decreased steamship journey times between the Atlantic and Pacific Oceans, it resulted in a much less dramatic redistribution of species.²⁸ Both canals represent significant bottlenecks to international trade; however, recently engineered expansions of both the Suez (2015) and Panama (2016) Canals to increase the flow of shipping have accelerated the introduction of alien marine fishes and other organisms between their adjacent waters.²⁹

The end of sail and the transition of maritime cargo transport to steel hulled steamships with watertight bulkheads not only led to faster travel by larger vessels and thus increased rates of global trade, but concomitantly introduced an effective means of alien species introductions through ballast water. Solid ballast (e.g., soil, rocks, gravel) had long been used to increase the stability of ocean-going vessels when cargo holds were empty, with the ballast unceremoniously dumped on the quayside at the port of arrival. Many alien plant and invertebrate species were introduced to new regions through solid ballast, but with few exceptions, they rarely spread beyond the port environment.³⁰ By 1880, the development of watertight bulkheads allowed the widespread use of ballast water tanks that were filled at the port of departure with marine, brackish, or freshwater as ballast and subsequently discharged at the port of arrival.³¹ However, many microorganisms, marine invertebrates, and fish picked up in ballast water were also discharged, leading to the introduc-

Figure 2. Cumulative number of regional trade agreements in force since 1950 The growth of bilateral and multilateral trade as depicted by the cumulative number of regional trade agreements in relation to the year in which the

agreement came into force (http://rtais.wto.org/).

tion of large numbers of alien species to coastal seas, estuaries, and freshwaters to the extent that the global movement of ballast water is now widely recognized as a leading cause of aquatic invasions worldwide.³² Currently, it is estimated that worldwide more than 7,000 marine species travel in the more than 3 million tonnes of ballast water that are transported every day by world shipping.33

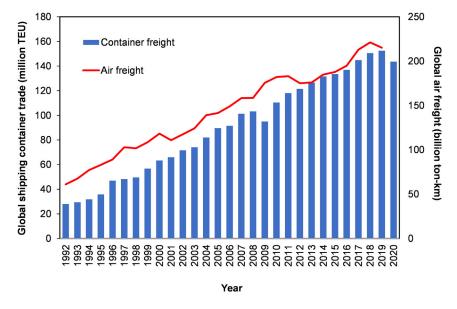
Another technological innovation with major trade implications was the equipping of vessels with refrigeration, which began

in earnest in the 1880s primarily for the transport of frozen meat but increasingly used to prolong the freshness of more delicate commodities, such as fruit.²⁴ For example, cool storage onboard vessels helped the international trade in bananas from Central America to the United States and Europe to grow dramatically from 1900 onward.34 Bananas are now grown commercially in more than 150 countries since refrigeration allows the product to reach distant markets, but shipments are notorious for concealing spiders and several species have become established as aliens in new regions following transport in bananas. 35 The growth in the movement of fresh produce facilitated by improved cool storage has provided opportunities for many pests and diseases to be shipped around the world. Indeed, many insect larvae can survive for several months at 4°C and thus international shipments of cold-stored fruit have facilitated the spread of alien pest insects.³⁶ Consequently, refrigerated cargo is often responsible for most alien species interceptions at international borders.37

The freight container is arguably one of the most important developments in international trade that has revolutionized the design of shipping vessels and ports helping integrate land and sea transport networks and so reduce shipping costs of a vast range of commodities.²⁵ The development of intermodalism, where the same container, with the same cargo, can be transported seamlessly between ships, trucks, and trains from an initial place of receipt to a final delivery point many kilometers away, has vastly increased the efficiency of trade. Transit times of containers at ports of arrival are markedly reduced, which facilitates higher survival rates and more rapid distribution of alien species away from ports, increasing propagule supply and invasion opportunity. Since the widespread adoption of standardized container designs in the 1960s, the growth in containerized transport has been spectacular (Figure 3). Today, the cargo handled by seaports is largely reflective of the economic complexity of their hinterlands with simple economies associated with bulk cargoes, while complex economies generate more containerized flows. 12 Containers have facilitated the trade in many commodities that would be difficult to transport

Review





otherwise, and these have changed the likelihood of introducing alien species. Once such commodity is used tires, awkward, bulky items that are costly to handle at the dockside. Containers made the trade in tires more cost-effective and opened up new sources in Asia for the growing market in Europe and the United States. 38 The Asian tiger mosquito (Aedes albopictus) can breed in residual water left inside used tires, and the conditions within a container are conducive to allow survival of desiccation-resistant eggs. As a consequence, this vector of several human diseases has become established in multiple new areas due to containerized international trade in used tires.³⁹ A further distinction with containerized trade, is that the container itself can be a vector for the introduction of alien pests, weeds, and pathogens. Containers have their own international travel itineraries, being loaded and unloaded at multiple ports since one container will be used multiple times to ship different products (Figure 4). Over time, cargo containers accumulate debris both internally and externally that facilitate the international transport of invertebrate adults, larvae and eggs, plant seeds, and pathogen spores that have the potential to lead to the establishment of economically important alien species in new regions.⁴⁰ During its lifetime, a single container will circumnavigate the globe multiple times such that the risk it might introduce an alien species into a new country rarely reflects only its most recent origin.

Commercial jet aviation began in the 1950s and initiated the global transport of freight by air. However, in terms of tonnage, air transportation carries an insignificant amount of freight (0.2% of total tonnage) compared with maritime transportation that handles about 90% of global trade. 12 Nevertheless, it remains one of the faster-growing sectors in international trade (Figure 3). In contrast to the important role in the introduction of pests, weeds, and pathogens into new regions that is played by the baggage carried by airline passengers, 41 air cargo plays a proportionally minor role in trade-related transport of alien species. Nevertheless, air cargo has assisted in the development of new trade in high-value products that need to be shipped relatively quickly across the world. The increased speed of transport

Figure 3. Growth in international air and sea freight

Characteristics of global freight trade depicting the growth since 1992 in global shipping container trade in million TEU (Twenty-foot Equivalent Units) (http:// uncatd.org/rmt), and a similar trend for air freight (https://data.wto.org/).

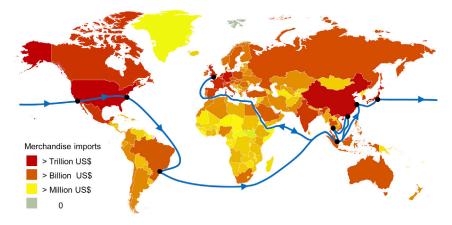
provides greater opportunity for the survival of alien species in air cargo, international airports provide quite different entry points to a new region compared with maritime ports, and the high-value products shipped by air represent different risks to commodities shipped in maritime trade. A wide range of potentially economically important alien insects have been intercepted on airline cargo, especially associated with plant products.42 The speed of airline cargo has led to a rapid increase in the international trade in fresh-

cut flowers since this commodity needs to be transported rapidly from the areas of production in tropical countries to consumers around the world (Figure 5A). However, fresh-cut flowers often also host many unwanted invertebrate species that may potentially establish as alien species in the importing country.4

From the 1850s onward, the telegraph has had a direct impact on the integration of global trade, and by the end of the 19th century, cables were established that not only linked Europe and the United States, but also the Far East and Australia.44 The telegraph had an enormous impact on global trade market integration, resulting in increased convergence in the prices of the same commodity worldwide, but also enabling commerce to respond more rapidly to changes in consumer demand.²⁴ The first transatlantic phone call took place in 1927 and ushered in an era of even faster communication. 11 By effectively shrinking geographic distance, the new telecommunication tools increased the volume of world trade and broadened the number of countries participating in international commerce as well as the types of commodities traded, outcomes that would also have increased the likelihood of alien species being transported to new regions.⁴⁵ Although parallels have been made between the telegraph and the Internet in terms of social impact, the latter has significantly democratized global trade, allowing individual citizens to participate as buyers and sellers of international products.⁴⁴ E-commerce sales worldwide are projected to reach an average of 40% of the global market share in 2026 and developing countries now account for the largest portion of new e-commerce. 46 Seeds and bulbs of plants are widely traded by small-scale producers and even individual hobbyists since they can be readily exported in large numbers and have a relatively high value-to-weight ratio. However, many plant species traded on the international Internet market are known to be invasive aliens in one or more regions of the world, with buyers often unable to identify the geographic origin of the sales due to the use of locally domiciled domain names of overseas suppliers.⁴⁷ International Internet trade is enhanced by express freight delivery often via air cargo, which increases the likelihood of species



One Earth Review



surviving transport and an increasing number of alien species are intercepted through this pathway at international borders. ⁴⁸ Most worryingly, is that often these consignments do not comply with phytosanitary requirements, and both prohibited alien species as well harmful organisms present as contaminants can easily be spread through Internet trade. ⁴⁹

Although not an exhaustive list of the technological changes that have increased the scale and velocity of international trade, these examples illustrate how each innovation has increased the opportunities for both the intentional and unintentional transport of alien species. Although the development of rail and road transport are important innovations that facilitate trade, they tend to occupy a more marginal portion of international transportation, since they are above all modes for national or regional transport services. 12 For example, less than 10% of the distance traveled by an average shipping container occurs by road or rail (Figure 4). Nevertheless, it would appear inevitable that the faster journey times by air and sea, transporting a greater volume and diversity of products from an increasing number of different countries, have led to a significant rise in the introduction of alien species. Despite the logic of this assumption, quantitative evidence for the role of international trade in biological invasions is surprisingly mixed.

INTERNATIONAL IMPORTS ARE A DIRECT DRIVER OF INVASIONS

Attempts to understand the role of trade in biological invasions either attempt to explain variation in the number of alien species in different countries in relation to the marked variation in economic metrics such as imports (Figure 4) or examine the change in alien species numbers over time in a single country and relate this to temporal change in economic parameters. For example, GDP has been a frequent metric used to explain variation among different countries in the number of alien species and often interpreted as an indication of the importance of international trade. 50-56 However, net exports (the value of exports minus imports) are only one component of GDP, and often represent a much smaller percentage than other components such as household spending, government spending, and investment. Thus, while economic growth may be an important driver of biological invasions, this may be due to many other factors unrelated to international trade. It follows that measures of trade

Figure 4. The itinerary of a single shipping container

Approximate global route (originating and ending at the port of Southampton, UK) of a single 40-foot shipping container monitored by the BBC for 421 days over which it covered 75,762 km by container ship, 5,197 km by train, and 2,171 km by road (www.bbc.co.uk/thebox). Countries are shaded in relation to the total value of merchandise imports in 2019 (https://data.wto.org/).

openness that represent the proportion of GDP captured by trade are also prone to misinterpretation since it is not always possible to disentangle the changes in economic growth from those due to changes in international trade (Figure 1).

It therefore appears more logical to examine the specific components of trade, such as imports, that have a direct link to alien species introductions.

Several studies that compared trends across multiple countries have found a positive relationship between the current value of merchandise imports (in US\$) and the total number of alien plants,⁵⁷ fungi,⁵⁸ or species listed on the Global Invasive Species Database. 59,60 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 (Figure 6). However, these types of analyses suffer from the difficulty of using a flow variable such as imports measured for a specific year to explain variation in a stock variable, such as alien species richness, that is a cumulative measure aggregated over many years. 61,62 This is analogous to using the velocity of a car at any one moment to estimate its long-term mileage. Why would the total number of alien species accumulated by a country over several centuries reflect contemporary imports? One way to reduce this problem is to ensure the trade and alien species records cover a similar time period. Thus the likelihood that an alien reptile established in the United States from 1999 onward was associated with the number of imports of each species as pets since that time. 63 Analyses of this kind can be relatively straightforward for contemporary records of alien species introductions, but are more challenging for records over longer time spans since a direct linear relationship between imports and alien species introductions over time may be unlikely. Nonlinearities may arise through a trade attenuation effect where increases in imports over time introduce progressively more of the potential global pool of alien species that might establish in the region to the extent that the rate of new introductions would decline over time.

To overcome these limitations, several approaches have attempted to model the accumulation of alien species over time using historical import data. For example, the accumulation of alien molluscs, plants, and pathogens over time in the United States was best described by a Michaelis-Menten model of cumulative value (US\$) of all merchandise imports. ¹⁸ An alternative modeling approach revealed that the introductions of insects over time in the United States could be described as a Poisson process modeled as an exponential function of the value (US\$) of agricultural imports. ⁶⁴ In this example, agricultural imports



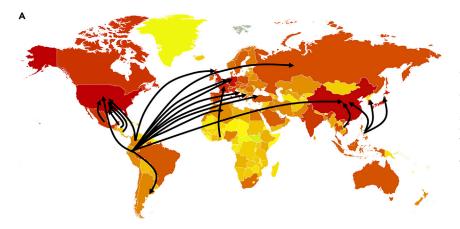
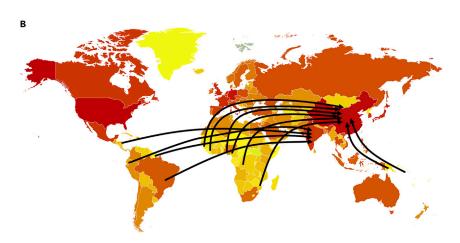




Illustration of the main trade flows in 2019 (https:// resourcetrade.earth) for: (A) Fresh-cut flowers, mostly originating from Latin America, are known to often be contaminated with alien species, and they represent an example where trade acts as a direct driver of invasions. (B) China and India are major importers of tropical timber that, because of unsustainable harvesting practices in the countries of origin, leads to fragmented and disturbed habitats that are vulnerable to invasion as an indirect result of international trade. Countries are shaded in relation to the total value of merchandise imports in 2019, as in Figure 4.



cantly associated with the number of pathogens and invertebrate pests of plants found in European countries and was again more important than climate similarity.67 A further study examined the global trade network of wild-caught birds and found that the risk of establishment of alien birds in the European Union was closely associated with the number of imported birds, diversity of import sources, and the network centrality of importer countries.⁶⁸ These three approaches on plants, invertebrates, and birds use measures of import intensity and connectivity between a source and destination region to predict the likelihood of an alien species being introduced. 13,67,68 This approach can also be adopted for the analysis of the role of imports in the introduction of specific alien species. The spread or ragweed (Ambrosia artemisiifolia) across Europe since 1950

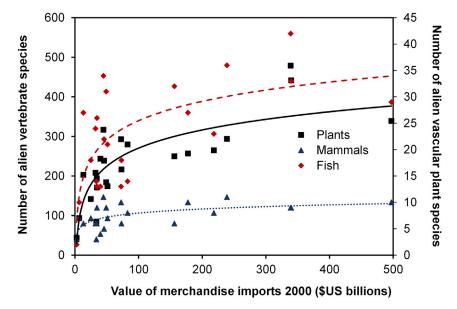
was associated with the bilateral volumes of imports of seed for sowing within the continent since the 1990s.⁶⁹ Genetic data and information on the bilateral volumes of beeswax imports have been combined to describe the role of international trade in the global spread of the small hive beetle (Aethina tumida) from its native range in Africa to other regions of the world. 70

The foregoing presents a strong case for the direct role of imports on the introduction of alien species but also shows that revealing this relationship is rarely straightforward. A potential concern is that studies continue to use different measures to characterize imports, either the value (US\$) or a volume (tonnage or numbers of individuals). The value of imports is relatively straightforward to aggregate across different commodities but it generally includes not only the cost of the goods when purchased by the importer, but also the cost of transport and insurance to the frontier of the importing country. About half of all global trade takes place between locations of more than 3,000 km apart and it is not uncommon for transport costs to account for 10% of the total cost of a product. 12 If goods transported from distant countries are more likely to be associated with alien species²³ but are also likely have higher transport costs, then a correlation between the risk of introduction and import value might arise. In addition, use of historical import

were viewed as a more likely pathway for insect introductions than total merchandise imports. A binomial rather than Poisson process was used to show that the arrival of plant pathogens in New Zealand over 133 years was significantly associated with the volume (tonnage) of commodities imported each year.⁶⁵ These models treat all imports similarly irrespective of their origin, but this may not be a sensible assumption if imports from certain regions pose a greater risk (Figure 5A). Historical data on annual import volumes (tonnage) from three different global source regions was used to model the accumulation of alien species over 140 years in the San Francisco Bay and highlighted that trade arising from the Western Pacific region posed the highest risk.66

Knowledge that the likelihood of the introduction of alien species varies by trading partner^{60,66} has led to studies examining wider bilateral trade relationships more thoroughly. Historical data describing trends of bilateral trade (measured as the value of exports in US\$) over 60 years was found to be a significant predictor of the geographic patterns in the global spread of alien plant species among 147 countries, even after climate matching between donor and recipient regions was considered. 13 A similar approach found that import connectivity (measured as the volume of live plant imports) among trading partners was signifi-





value data should account for the marked decline in transport costs over the past 2 centuries, ²⁴ and especially since the advent of containerization in the 1950s. ²⁵ Furthermore, value and volume may not be correlated, as in the case of air transportation that in terms of tonnage carries an insignificant amount of global freight (0.2% of total tonnage) but accounts for 15% of the value of global trade. ¹²

Aggregated indices of total merchandise value ignore the fact that different commodities pose varying risks and that these risks do not scale with the value of the commodity. Machinery and equipment account for over 40% of the value of merchandise trade, followed by oil and mining products (20%) and chemicals (13%), with agricultural commodities accounting for only 12% of the value of world merchandise trade (Figure 7). Yet trade in live plants and agricultural products has often been signaled as one of the most important introduction pathways. 71,72 In these particular circumstances, it makes sense to focus on the primary commodities (e.g., live plants) that are most likely to be associated with the introduction of specific groups of alien species of interest (e.g., phytophagous insects) rather than aggregated metrics, and to use the volume rather than value imported.

Not all alien species introductions will be associated with a specific commodity, but may enter a region 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. 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 biological invasions in several maritime ecoregions. Shipping traffic volumes were more than twice as high on routes connecting the historical distribution of the Asian tiger mosquito to ports where it has established in comparison with routes to climatically similar ports where the species is absent. Nevertheless, in this study, greater granularity in the shipping data would have proven useful, since for mosquitoes, container shipping would play a

Figure 6. Imports and the number of alien species

Nonlinear relationships between the value of merchandise imports (https://data.wto.org/) in 2000 and the number of alien vascular plants, mammals, and fish recorded in 23 European countries prior to 2005. Fagression equations for each taxon are as follows: mammals (y = 5.27 ln(x) + 1.20, $R^2 = 0.47, p < 0.01$), fish (y = 1.12 ln(x) + 2.86, $R^2 = 0.36, p < 0.01$) and plants (y = 66.23 ln(x) - 34.52, $R^2 = 0.67, p < 0.001$).

much more significant role in transport than bulk carriers or oil tankers. However, despite the importance of shipping containers as sources of the introduction of alien species, ⁴⁰ no study to date has attempted to relate contemporary risk of biological invasions to variation in the number of containers imported or indeed their global itineraries. Given the 5-fold increase over the past 30 years in the number of

shipping containers carrying international trade (Figure 3) and the risk containers pose, this would appear to be a major gap in current knowledge of alien invasion risks through international trade.

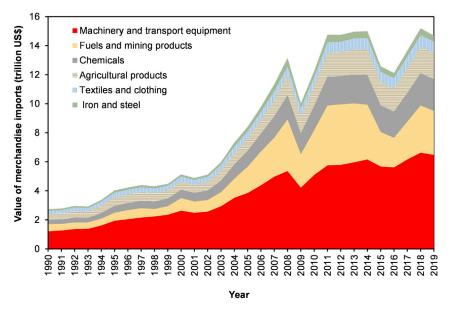
INTERNATIONAL TRADE IS AN INDIRECT DRIVER OF INVASIONS

Although international trade is clearly an important and necessary direct driver of the introduction of alien species into new regions, it is widely understood that other drivers also play a role. Several studies examining the role of international imports on the number of alien species have reported that other factors, such as the Human Development Index, resource extraction, and pollution, also play a role in explaining the observed patterns. ^{57,60} To date, these drivers are often considered separately with no examination of interactions between the level of imports and other variables that also can influence biological invasions. However, although international trade is a direct driver of biological invasions, it may also act indirectly through other drivers to further influence the number of alien species established in a region. Here, the indirect role international trade plays in the introduction and spread of alien species is illustrated through its influence of five drivers of biological invasions (Figure 8): natural resource extraction, pollution, climate change, land-use change, and urbanization.

Due to the uneven distribution of natural resources worldwide and different levels of industrial development across the world, international trade has been vital to link areas rich in natural resources to regions of consumption. Natural resources extraction includes timber harvesting in natural forests (Figure 5B), the mining of mineral ores, and extraction of fossil fuels. By facilitating resource extraction, international trade has also acted as a driver of environmental degradation, especially where market prices do not account for the value of natural capital and ecosystems services involved. 75,76 A further consequence of resource extraction is the increased likelihood of alien species introduction and establishment due to removal of vegetation and soil

Review





perturbation that provides suitable sites for colonization, which then interacts with increased vehicular traffic (e.g., logging trucks, mine excavators) that can unintentionally deposit alien organisms contained in mud and soil that has been transported over long distances.77,78

Although natural resource extraction generates considerable local pollution, international trade is also widely understood to be a major contributor to global atmospheric pollution. 79 The emissions from international sea transportation release ozone. sulfate, nitrogen compounds, carbon dioxide, volatile organic compounds, and particulate matter into the atmosphere that have transboundary effects across continental landmasses as well as increase ocean acidification in coastal areas.⁸⁰ In addition, the production of goods for international export generates additional atmospheric pollution that has both local and longdistance effects.81-83 Atmospheric deposition of nitrogen compounds can have dramatic effects on recipient ecosystems where critical loads are breached and can lead to increased numbers and distributions of alien species.84,85

A major pollutant produced as a result of international trade is carbon dioxide, a potent greenhouse gas. Emissions of carbon dioxide from the production of traded goods and services have increased from 20% of global emissions in 1990 to 26% in 2008.86 In addition, emissions from trade-related movement of commodities account for 40% of all greenhouse gases emitted from all forms of transport worldwide. 46 Carbon dioxide emissions embodied in trade have a significant impact on participation in and effectiveness of global climate policies, such as the Kyoto Protocol.⁸⁷ The significant contribution of international trade through embedded carbon dioxide emissions will feed through to future climate change. Although not all alien species will benefit, in general climate change is expected to increase the rate at which alien species are introduced into new regions, facilitate population expansion in invaded ranges, and lead to greater impacts on biodiversity and ecosystem services.88-91 For example, the Asian tiger mosquito has been transported worldwide by international trade but has only established where

Figure 7. Components of merchandise trade over time

Temporal trend in the value of different components of merchandise trade since 1990 (https://data.wto. org/) illustrating the dominance of machinery and transport equipment in international trade and the slowing down of trade growth since 2010.

the climate is suitable, relaxing this barrier through climate change would lead to many more introductions of this species.⁷⁴ Studies that have forecast the impacts of international trade and climate change on biological invasions have found that although both interact to shape future risk, it is the former that appears most important. 13,67

The extensive clearing of tropical forests throughout past decades is in part driven by increased international trade in agricultural commodities (Figure 5B), and the

expectation is that this trend will continue due to further trade liberalization. 92,93 Increasing global demands for meat, animal feed, and oil seed products have led to major changes in land use in developing countries.⁹⁴ 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. 95 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.96 Deforestation is a primary contributor to climate change, but the resulting fragmentation of tropical forests also increases their vulnerability to invasions by alien species. 97-99 In addition, new crops such as the African oil palm (Elaeis guineensis) can themselves spread beyond cultivated areas to become invasive alien species in regions where they are not native. 100 The growth of urban areas also results in land-use change, as natural and agricultural areas are fragmented and converted to housing, and this environmental disturbance favors the persistence of generalist human commensal species drawn from around the world. 101

Urbanization encompasses the processes that lead to the development of urban areas and consequently the depopulation of rural areas and the factors that determine the spatial and size distribution of cities. It is projected that urban populations will increase by five billion by 2030 with direct impacts on the natural environment. 102 International trade is an important driver of urbanization since it encourages the agglomeration of economic activities (and hence labor) in specific urban areas, particularly where these are associated with international transport hubs, such as marine ports, airports, or national borders. 103-105 Cities that have greater number of global trade links tend to be highly urbanized, and this increases with the level of agricultural imports and exports of non-agricultural commodities. 106 Urban areas also represent hotspots of alien species richness, which in part can be explained by the high rate of deliberate introductions of alien species either for





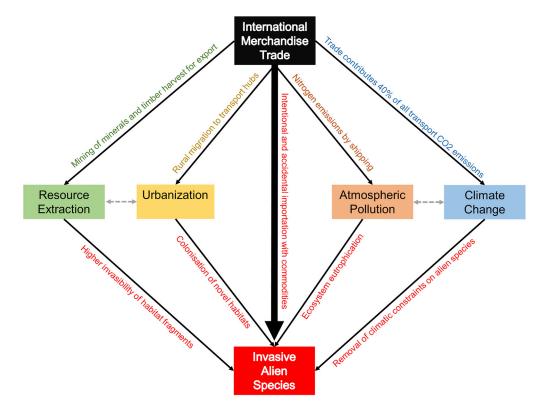


Figure 8. Linking direct and indirect effects of trade on invasions

Schematic illustration of the direct (though the transport of alien species) and indirect (through resource exploitation, urbanization, atmospheric pollution, and climate change) roles international merchandise trade plays in the introduction and spread of invasive alien species.

amenity value (e.g., street trees) or as pets (e.g., parrots) that subsequently escape, and also the higher international connectivity of large cities that facilitates unintentional introductions of alien species via ports and airports. ^{107,108} In the marine realm, urbanized maritime infrastructure associated with ports (e.g., breakwaters, jetties, and seawalls) does not function as a surrogate of natural rocky habitats but instead facilitates the establishment and spread of alien species. ¹⁰⁹ For example, in coastal North America, approximately 90% of the alien species inhabiting hard substrata have been reported from docks and marinas. ¹¹⁰ 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.

These five examples of indirect effects of international trade on biological invasions are not exhaustive. For example, natural resource extraction, urbanization, harvesting of native forests, and the expansion of agricultural land are also important contributors to the GDP of a country, 111 which has frequently been found to correlate with total numbers of alien species. 50-54 However, while indirect effects of international trade on biological invasions undoubtedly occur, suitable analyses to document these effects have not been undertaken. Quantifying the indirect role of international trade on biological invasions through climate change and atmospheric pollution will be difficult due to the diffuse, transboundary chain of causation. Time series data will be required to examine the role of

international trade on rates of urbanization, land-use change, and resource extraction, and associated changes in the number of alien species. Without such information, it is conceivable that the contemporary focus on imports as a direct driver of biological invasions may be missing much larger threats posed by indirect effects (Figure 8).

INTERNATIONAL TRADE REGULATION CAN REDUCE INVASION RISK

Attempts to curb the introduction of alien species introductions through international trade have a long history with quarantine and inspection services designed to protect agricultural crops established as early as 1899 in the Netherlands, 1902 in Australia, and 1912 in the United States. 15 International initiatives include the establishment of the World Organization for Animal Health in 1921 and the International Plant Protection Convention in 1952, both of which commit most nations in the world to binding agreements regarding surveillance and reporting to prevent the spread of alien species injurious to agriculture. 112 More recently, the International Convention for the Control and Management of Ships' Ballast Water and Sediments entered into force in 2017 and in the long-term should significantly reduce the inadvertent transport of invasive alien species in ballast water. 113 Potentially, these initiatives should have weakened the relationship between the flow of imports and the introduction of alien species, but is there any evidence that this is the case?

Review



It might be expected that quarantine inspections of imported commodities at international borders would be effective in limiting the rate at which alien species enter a country. Comparisons of alien species intercepted by quarantine inspectors with species known to have established over the same period suggest otherwise. Analysis of almost 2 decades of quarantine inspection data from Australia (1986-2005) and South Korea (1996-2014) similarly showed that most alien insect species that successfully mounted an incursion had not been intercepted at the border over the same period. 114,115 Thus, despite the best efforts of quarantine inspectors and high investment in commodity inspections, alien species continue to slip through the border. Depending on the commodity concerned, slippage rates have been found to range from 22% to 52% for alien ant introductions to New Zealand, 116 and as much as 50% to 98% for alien insects in the United States.³⁷ Large international differences in inspection intensity and variation in the probability that the inspections could detect a level of infestation below 1% have been found in Europe. 117 One reason for these high slippage rates is simply the failure of government investment in guarantine to keep up with the increasing levels of commodity imports. Because the number of sea cargo containers arriving at ports each year often number in the millions, only a fraction of containers can be inspected. It has been estimated that to increase the inspection rate of containers from the standard 2% to a more effective 5% at the Port of New York and New Jersey would require an additional 400 inspectors at an additional cost of US\$1.2 million per month. 15 However, there is also evidence that the inspection process is suboptimal, potentially biased toward commodities from low-income countries irrespective of their actual biosecurity risk, and focused on historically important risk goods and alien species rather than contemporary risks. 118

Nevertheless, even if not 100% effective, implementation of border quarantine may still reduce the risk of alien species introductions and may also act as a deterrent to other nations that might otherwise export contaminated commodities. This appears to be the case in New Zealand, where the rate of arrival of plant pathogens declined after the establishment of stricter biosecurity controls at the border in the 1990s, but even here the magnitude of the effect varied with the agricultural sector concerned. 65 Thus, implementation of guarantine and inspection procedures at international borders is likely to change the relationship between the volume or value of imports and the risk of introducing alien species. A marked example of this phenomenon is in the worldwide trade in wild-caught birds, where the invasion risk of a country was initially associated with its degree of connectivity in the global trade network, but this relationship disappeared after 2005 when the European Union banned all imports of wild-caught birds, which resulted in a major change in the global trade network and lower risks as a result of re-routed trade flows.⁶⁸ European regulations implemented in 2008 that limit the use of alien species in aquaculture and set strict quarantine regulations also appear to have been effective in reducing introductions of alien species via this trade route into European seas. 119 A further illustration of how risk management can influence invasion risk is provided by livestock diseases. Outbreaks of livestock disease listed by the World Organization for Animal Health as being of relatively low impact reveal a positive association with levels of imports into a country, but for more harmful diseases the relationship is negative and has been interpreted as reflecting the implementation of more stringent sanitary procedures for the most costly pathogens. 62 The evidence that relatively recent biosecurity regulations at national borders have the potential to alter the relationship between imports and the risk of biological invasions implies that it may be unwise to simply extrapolate future risks based only on the growth of trade without also accounting for potential increases in the efficacy of quaratine interventions. Nevertheless, while it appears that national and international policies can be effective in mitigating some components of trade-related risk of biological invasions, as they stand, current regulations are probably insufficient to address an increase in threats from alien species in the future.

BIOLOGICAL INVASIONS TRADE AWAY OUR SUSTAINABLE FUTURE

Temporal trends in the volume of global trade reveal a period of progressive growth up until the 1980s, followed by a phase of accelerated increase (1980-2000) led by emerging economies, and then reaching peak growth (2000-2020) where both the global value of merchandise trade (Figure 7) and the share of global GDP accounted for by imports (Figure 1) have begun to plateau. Could the leveling-off in globalization result in reduced rates of alien species introductions through trade? This appears unlikely. Several studies have used the value of merchandise imports over the period of peak globalization (from 2000 onward) to predict future risks worldwide and found that assuming current levels of global trade, the risk of alien species introductions remains high. 120-122 Worryingly, these predictions may underestimate future risk. Rather than a leveling-off of global trade, global demand for freight transport is projected to grow dramatically over the next 3 decades, with maritime trade volumes tripling by 2050 and significant growth in air cargo. 46 Shipping growth will have a far greater effect on marine invasions than climatedriven environmental changes, and the emerging global shipping network could yield a 3- to 20-fold increase in global invasion risk by 2050. 123 But in addition to increased volumes of freight, the geography of global trade is also expected to change significantly by 2050. The growth of regional trade agreements shows little sign of leveling-off (Figure 2) and increased moves toward free trade will likely lead to a larger volume and diversity of commodities being transported around the world. Furthermore, the biological invasions currently faced by countries may be a legacy of historical trade due to lag effects between economic growth and subsequent invasion, 124 thus the consequences of recent trade developments may not be experienced until many years in the future.

Just as the Suez Canal led to a step change in international trade routes, so will climate change. Increasing melting ice cover over the Arctic Sea has created new possibilities for commercial shipping and, although likely to only carry a small fraction of global freight, the Northern Sea Route is predicted to become ice-free on a seasonal basis by 2050.46 The Northern Sea Route could reduce distances traveled by maritime shipping from northern European ports to Korea by 31% and to China by 23% relative to routing through the Suez Canal. 125 Shorter voyages could favor survival of alien species found as contaminants of commodities or stowaways in shipping containers that would



otherwise perish when exposed to higher temperatures experienced on shipping routes that currently pass through the tropics. ¹²⁶

The geopolitical dimension of international trade is rapidly changing with emerging economies playing a greater role in the future. Today, over half of all international merchandise trade involves at least one developing country. 127 The Boosting Intra-Africa Trade action plan of the African Union and the Trade Facilitation Agreement of the World Trade Organization seek to increase regional trade integration in Africa through improved road, rail, and maritime transport. 46 Many developing countries, including several in Africa, are included in the Belt and Road Initiative led by China, which seeks to improve transport infrastructure and increase trade flows by sea and land among participating countries. Projections of the future risk of invasions arising from the Belt and Road Initiative indicate an increased risk of alien species introductions as a direct result of increased trade. 122 In addition, future construction of road and rail infrastructure, the building of larger and deeper harbors, the resulting human migration from rural areas to these growing urban transport hubs, and the increased pressure on natural resources to supply international demand will certainly increase the indirect effects of international trade on the establishment and spread of invasive alien species.

Given the increase in volume of freight as well as the changing geography of international trade, it seems sensible to assume that alien species will continue to be introduced via commodity imports at a rate equal, if not greater, than experienced in the past. International trade will introduce new source pools of alien species into the global transport of commodities and increase the risk of spreading emerging alien species that have never been recorded outside of their native range before.²³ Is there any potential to mitigate the high risk of future biological invasions through international trade? Most governments have implemented measures to detect, intercept, eradicate, or control pests, weeds, or pathogens of agricultural importance under the auspices of international bodies such as the World Organization for Animal Health and International Plant Protection Convention. However, as has been shown with border inspection data, 114,118 the effectiveness of interventions is quite variable, even among developed economies. The outlook for preventing future introductions of invasive alien species that primarily affect biodiversity is even less promising. Despite the Convention on Biological Diversity setting out among its Aichi Biodiversity Targets a clear goal to address the identification and prioritization of pathways for the introduction of invasive alien species by 2020, only 10% of reporting parties have national targets to address this risk and are on track to meet them. 128 There also remain many significant political, administrative, legal, technical, and maritime challenges to adequately implementing the International Convention for the Control and Management of Ships' Ballast Water and Sediments. 129

A step change is needed to address the significant risks of future biological invasions arising from both the direct and indirect effects of international trade. One option would be to advance the concept of One Biosecurity, an interdisciplinary approach to biosecurity policy and research that enhances the interconnections among human, animal, plant, and envi-

ronmental health to prevent and mitigate the impacts of invasive alien species. 112 Although specific traded commodities and transport vectors pose different risks to human, animal, plant, and environmental health, they require a similar approach to biosecurity management. Ballast water discharges are a direct effect of international trade on biological invasions, but in addition to introducing alien marine species that impact negatively on biodiversity and aquaculture production, ballast water can transfer the toxigenic cholera pathogen (Vibrio cholerae O1) from one harbor to another. 130 Similarly, the indirect effect of deforestation due to international trade can facilitate the introduction and spread of invasive alien organisms but also augments the risk of emerging zoonotic pathogen outbreaks as humans increasingly interact with forest wildlife. A more unified approach to biosecurity will facilitate and ensure cross-fertilization of best practice among the different disciplines, as well as deliver more cost-effective management by avoiding duplication of roles and activities. A key outcome arising from One Biosecurity would be a more coordinated focus on dealing with the pandemic risks of invasive alien species through the early identification and management by governments of alien species within their territory that have the potential to spread across multiple continents. 113 New assessment methods would need to be developed to identify future pandemic biosecurity risks and there would have to be a stronger regulatory framework to ensure governments comply with surveillance and reporting requirements, which would entail greater investment in capacity building across the world, but these could all be achieved within a decade. 113 The central issue is the international appetite to repair the currently fractured and limited multilateral agreements addressing biosecurity and the commitment of governments and industry to more sustainable and cleaner trade. To date, discussions on the sustainability of trade have largely focused on the displacement of environmental and social impacts from developed to developing countries, particularly in relation to the production of greenhouse gases and other pollutants that harm human health. 79 A first step might be to make the most of the continuing growth in regional trade agreements worldwide (Figure 2) to establish stronger regulations to diminish the risk of introducing invasive alien species among trading partners at a regional scale. Nevertheless, the growing threat of international trade as a direct and indirect driver of biological invasions cannot be underestimated, and global action through multilateral agreements at a global rather than regional scale will be required to avoid the future long-term legacies of emerging alien species on food security, biodiversity loss and human health.

ACKNOWLEDGMENTS

The author thanks two anonymous referees for constructive comments on an earlier version of the manuscript.

REFERENCES

 Richardson, D.M., Pyšek, P., and Carlton, J.T. (2011). A compendium of essential concepts and terminology in invasion ecology. In Fifty Years of Invasion Ecology: The Legacy of Charles Elton, D.M. Richardson, ed. (Wiley), pp. 409–420.

Review



- 2. Essl, F., Bacher, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kowarik, I., Kühn, I., Pyšek, P., Rabitsch, W., et al. (2018). Which taxa are alien? Criteria, applications, and uncertainties. Bioscience 68, 496-509.
- 3. Hulme, P.E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., et al. (2008). Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J. Appl. Ecol. 45, 403-414.
- 4. Hulme, P.E. (2015). Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. J. Appl. Ecol. 52, 1418-1424.
- 5. Essl, F., Bacher, S., Blackburn, T.M., Booy, O., Brundu, G., Brunel, S., Cardoso, A.C., Eschen, R., Gallardo, B., Galil, B., et al. (2015). Crossing frontiers in tackling pathways of biological invasions. Bioscience 65,
- 6. Hulme, P.E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10-18.
- 7. Jenkins, P.T. (1996). Free trade and exotic species introductions. Conserv. Biol. 10, 300-302.
- 8. Perrings, C., Dehnen-Schmutz, K., Touza, J., and Williamson, M. (2005). How to manage biological invasions under globalization. Trends Ecol. Evol. 20, 212-215.
- Saul, W.C., Roy, H.E., Booy, O., Carnevali, L., Chen, H.J., Genovesi, P., Harrower, C.A., Hulme, P.E., Pagad, S., Pergl, J., et al. (2017). Assessing patterns in introduction pathways of alien species by linking major invasion data bases. J. Appl. Ecol. 54, 657–669.
- 10. Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., et al. (2020). Scientists' warning on invasive alien species. Biol. Rev. 95, 1511-1534.
- 11. Parker, P. (2021). History of World Trade in Maps (HarperCollins Publishers Limited).
- 12. Rodrigue, J.P. (2020). The Geography of Transport Systems (Routledge).
- 13. Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M., et al. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. Glob. Change Biol. 21, 4128-4140.
- 14. Poon, J.P.H., and Rigby, D.L. (2017). International Trade: The Basics (Taylor & Francis Group).
- 15. Hulme, P.E. (2014). An introduction to plant biosecurity: past, present and future. In The Handbook of Plant Biosecurity, G. Gordh and S. McKirdy, eds. (Springer), pp. 1-25.
- 16. Bradley, B.A., Blumenthal, D.M., Early, R., Grosholz, E.D., Lawler, J.J., Miller, L.P., Sorte, C.J., D'Antonio, C.M., Diez, J.M., Dukes, J.S., et al. (2012). Global change, global trade, and the next wave of plant invasions. Front. Ecol. Environ. 10, 20–28.
- 17. Liebhold, A.M., Brockerhoff, E.G., and Kimberley, M. (2017). Depletion of heterogeneous source species pools predicts future invasion rates. J. Appl. Ecol. *54*, 1968–1977.
- 18. Levine, J.M., and D'Antonio, C.M. (2003). Forecasting biological invasions with increasing international trade. Conserv. Biol. 17, 322-326.
- 19. Fouquin, M., and Hugot, J. (2016). Two Centuries of Bilateral Trade and Gravity Data: 1827-2014 (CEPII), Working Paper 2016.
- 20. Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., et al. (2017). No saturation in the accumulation of alien species worldwide. Nat. Commun. 8, 14435.
- 21. Preston, C.D., Pearman, D.A., and Hall, A.R. (2004). Archaeophytes in Britain. Bot. J. Linn. Soc. 145, 257-294.
- 22. Parker, P. (2012). The Great Trade Routes: A History of Cargoes and Commerce over Land and Sea (Naval Institute Press).
- 23. Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., van Kleunen, M., Winter, M., et al. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. Proc. Natl. Acad. Sci. U S A 115, E2264-E2273.
- 24. O'Rourke, K.H., and Williamson, J.G. (2001). Globalization and History: The Evolution of a Nineteenth-Century Atlantic Economy (MIT Press).
- 25. Levinson, M. (2008). The Box: How the Shipping Container Made the World Smaller and the World Economy Bigger (Princeton Univer-
- 26. Shah, S. (2016). Pandemic: Tracking Contagions, from Cholera to Ebola and beyond (Farrar, Straus and Giroux).

- 27. Galil, B.S., Mienis, H.K., Hoffman, R., and Goren, M. (2020). Non-indigenous species along the Israeli Mediterranean coast: tally, policy, outlook. Hydrobiologia 19, 1–9.
- 28. Ros, M., Ashton, G.V., Lacerda, M.B., Carlton, J.T., Vázquez-Luis, M., Guerra-García, J.M., and Ruiz, G.M. (2014). The Panama canal and the transoceanic dispersal of marine invertebrates: Evaluation of the introduced amphipod Paracaprella pusilla Mayer, 1890 in the Pacific Ocean. Mar. Environ. Res. 99, 204-211.
- 29. Castellanos-Galindo, G.A., Robertson, D.R., and Torchin, M.E. (2020). A new wave of marine fish invasions through the Panama and Suez canals. Nat. Ecol. Evol. 4, 1444-1446.
- 30. Mack, R.N. (2003). Global plant dispersal, naturalization, and invasion: pathways, modes, and circumstances. In Invasive Species: Vectors and Management Strategies, G. Ruiz and J. Carlton, eds. (Island Press), pp. 3-30.
- 31. Carlton, J.T. (2011). Ballast. In Encyclopedia of Biological Invasions, D. Simberloff and M. Rejmanek, eds. (University of California Press), pp. 43-49.
- 32. Carlton, J.T., and Ruiz, G.M. (2005). The magnitude and consequences of bioinvasions in marine ecosystems. In Marine Conservation Biology, E.A. Norse and L.B. Crowder, eds. (Island Press), pp. 123-148.
- 33. World Health Organization. (2011). Guide to Ship Sanitation (World Health Organization).
- 34. Lennerfors, T.T., and Birch, P. (2019). Snow in the Tropics: A History of the Independent Reefer Operators (Brill).
- 35. Vetter, R.S., Crawford, R.L., and Buckle, D.J. (2014). Spiders (Araneae) found in bananas and other international cargo submitted to North American arachnologists for identification. J. Med. Entomol. 51, 1136-1143.
- 36. Mangan, R.L., and Hallman, G.J. (1998). Temperature Treatments for Quarantine Security: New Approaches for Fresh Commodities (Westview Press. Inc.).
- 37. Work, T.T., McCullough, D.G., Cavey, J.F., and Komsa, R. (2005). Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol. Invasions 7, 323-332.
- 38. Reiter, P., and Sprenger, D. (1987). The used tire trade a mechanism for the worldwide dispersal of container breeding mosquitos. J. Am. Mosq. Contr. Assoc. 3, 494-501.
- 39. Hawley, W.A., Reiter, P., Copeland, R.S., Pumpuni, C.B., and Craig, G.B. (1987). Aedes albopictus in North America - probable introduction in used tires from northern Asia. Science 236, 1114-1116.
- 40. Stanaway, M.A., Zalucki, M.P., Gillespie, P.S., Rodriguez, C.M., and Maynard, G.V. (2001). Pest risk assessment of insects in sea cargo containers. Aust. J. Entomol. 40, 180-192.
- 41. McCullough, D.G., Work, T.T., Cavey, J.F., Liebhold, A.M., and Marshall, D. (2006). Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol. Invasions 8, 611-630.
- 42. Caton, B.P., Dobbs, T.T., and Brodel, C.F. (2006). Arrivals of hitchhiking insect pests on international cargo aircraft at Miami international airport. Biol. Invasions 8, 765-785.
- 43. Areal, F.J., Touza, J., MacLeod, A., Dehnen-Schmutz, K., Perrings, C., Palmieri, M.G., and Spence, N.J. (2008). Integrating drivers influencing the detection of plant pests carried in the international cut flower trade. J. Environ. Manage. 89, 300-307.
- 44. Standage, T. (2018). The Victorian Internet: The Remarkable Story of the Telegraph and the Nineteenth Century's On-Line Pioneers (Bloomsbury Publishing).
- 45. Lew, B., and Cater, B. (2006). The telegraph, co-ordination of tramp shipping, and growth in world trade, 1870-1910. Eur. Rev. Econ. Hist. 10, 147-173.
- 46. International Transport Forum (2019). ITF Transport Outlook 2019 (OECD).
- 47. Humair, F., Humair, L., Kuhn, F., and Kueffer, C. (2015). E-commerce trade in invasive plants. Conserv. Biol. 29, 1658-1665.
- 48. Pearson, H.G., and Hill, R.L. (2014). Risks for New Zealand's biosecurity from internet trading of plants. 19th Australasian Weeds Conference, Science, Community and Food Security: The Weed Challenge (Tasmanian Weed Society), pp. 182-185.
- 49. Kaminski, K., Beckers, F., and Unger, J.G. (2012). Global internet trade of plants - legality and risks. Bull. OEPP 42, 171-175.
- 50. Carpio, A.J., De Miguel, R.J., Oteros, J., Hillström, L., and Tortosa, F.S. (2019). Angling as a source of non-native freshwater fish: a European review. Biol. Invasions 21, 3233-3248.



One Earth Review

- Rojas-Sandoval, J., Ackerman, J.D., and Tremblay, R.L. (2020). Island biogeography of native and alien plant species: contrasting drivers of diversity across the Lesser Antilles. Divers. Distrib. 26, 1539–1550.
- Amano, T., Coverdale, R., and Peh, K.S.H. (2016). The importance of globalisation in driving the introduction and establishment of alien species in Europe. Ecography 39, 1118–1128.
- Carpio, A.J., Álvarez, Y., Oteros, J., León, F., and Tortosa, F.S. (2020). Intentional introduction pathways of alien birds and mammals in Latin America. Glob. Ecol. Conserv. 22, e00949.
- Bebber, D.P., Holmes, T., Smith, D., and Gurr, S.J. (2014). Economic and physical determinants of the global distributions of crop pests and pathogens. New Phytol. 202, 901–910.
- Dawson, W., Moser, D., Van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., and Blackburn, T.M. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. Nat. Ecol. Evol. 1, 0186.
- Hulme, P.E. (2007). Biological invasions in Europe: drivers, pressures, states, impacts and responses. In Biodiversity under Threat, R.E. Hester and R.M. Harrison, eds. (RSC Publishing), pp. 56–80.
- Vila, M., and Pujadas, J. (2001). Land-use and socio-economic correlates of plant invasions in European and North African countries. Biol. Conserv. 100, 397–401.
- Deprez-Loustau, M.-L. (2009). Alien fungi in Europe. In Handbook of Alien Species in Europe, DAISIE., ed. (Springer), pp. 15–28.
- Westphal, M.I., Browne, M., MacKinnon, K., and Noble, I. (2008). The link between international trade and the global distribution of invasive alien species. Biol. Invasions 10, 391–398.
- Dalmazzone, S., and Giaccaria, S. (2014). Economic drivers of biological invasions: a worldwide, bio-geographic analysis. Ecol. Econ. 105, 154–165.
- Dalmazzone, S. (2000). Economic factors affecting vulnerability to biological invasions. In The Economics of Biological Invasions, C. Perrings, S. Dalmazzone, and M.H. Williamson, eds. (Edward Elgar Publishing), pp. 17–30.
- Perrings, C. (2010). Exotic effects of capital accumulation. Proc. Natl. Acad. Sci. U S A 107, 12063–12064.
- Stringham, O.C., and Lockwood, J.L. (2018). Pet problems: biological and economic factors that influence the release of alien reptiles and amphibians by pet owners. J. Appl. Ecol. 55, 2632–2640.
- Hlasny, V., and Livingston, M. (2008). Economic determinants of invasion and discovery of nonindigenous insects. J. Agric. Appl. Econ. 40, 1.
- 65. Sikes, B.A., Bufford, J.L., Hulme, P.E., Cooper, J.A., Johnston, P.R., and Duncan, R.P. (2018). Import volumes and biosecurity interventions shape the arrival rate of fungal pathogens. PLoS Biol. 16, e2006025.
- Costello, C., Springborn, M., McAusland, C., and Solow, A. (2007). Unintended biological invasions: does risk vary by trading partner? J. Environ. Econ. Manag. 54, 262–276.
- Chapman, D., Purse, B.V., Roy, H.E., and Bullock, J.M. (2017). Global trade networks determine the distribution of invasive non-native species. Glob. Ecol. Biogeogr. 26, 907–917.
- Reino, L., Figueira, R., Beja, P., Araújo, M.B., Capinha, C., and Strubbe, D. (2017). Networks of global bird invasion altered by regional trade ban. Sci. Adv. 3, e1700783.
- Chapman, D.S., Makra, L., Albertini, R., Bonini, M., Páldy, A., Rodinkova, V., Sikoparija, B., Weryszko-Chmielewska, E., and Bullock, J.M. (2016). Modelling the introduction and spread of non-native species: international trade and climate change drive ragweed invasion. Glob. Change Biol. 22, 3067–3079.
- Idrissou, F.O., Huang, Q., Yañez, O., and Neumann, P. (2019). International beeswax trade facilitates small hive beetle invasions. Sci. Rep. 9, 1–10.
- Liebhold, A.M., Brockerhoff, E.G., Garrett, L.J., Parke, J.L., and Britton, K.O. (2012). Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front. Ecol. Environ. 10, 135–143.
- Eschen, R., Douma, J.C., Grégoire, J.C., Mayer, F., Rigaux, L., and Potting, R.P. (2017). A risk categorisation and analysis of the geographic and temporal dynamics of the European import of plants for planting. Biol. Invasions 19, 3243–3257.
- Seebens, H., Schwartz, N., Schupp, P.J., and Blasius, B. (2016). Predicting the spread of marine species introduced by global shipping. Proc. Natl. Acad. Sci. U S A 113, 5646–5651.
- Tatem, A.J., Hay, S.I., and Rogers, D.J. (2006). Global traffic and disease vector dispersal. Proc. Natl. Acad. Sci. U S A 103, 6242–6247.

- Mayer, A., and Haas, W. (2016). Cumulative material flows provide indicators to quantify the ecological debt. J. Polit. Ecol. 23, 350–363.
- Huang, S., An, H., Viglia, S., Buonocore, E., Fang, W., and Ulgiati, S. (2017). Revisiting China-Africa trade from an environmental perspective. J. Clean. Prod. 167, 553–570.
- Bergquist, E., Evangelista, P., Stohlgren, T.J., and Alley, N. (2007). Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environ. Monit. Assess. 128, 381–394.
- Walsh, P.D., Henschel, P., Abernethy, K.A., Tutin, C.E., Telfer, P., and Lahm, S.A. (2004). Logging speeds little red fire ant invasion of Africa. Biotropica 36, 637–640.
- Wiedmann, T., and Lenzen, M. (2018). Environmental and social footprints of international trade. Nat. Geosci. 11, 314–321.
- Endresen, Ø., Sørgård, E., Sundet, J.K., Dalsøren, S.B., Isaksen, I.S., Berglen, T.F., and Gravir, G. (2003). Emission from international sea transportation and environmental impact. J. Geophys. Res. Atmos. 108, D17.
- Oita, A., Malik, A., Kanemoto, K., Geschke, A., Nishijima, S., and Lenzen, M. (2016). Substantial nitrogen pollution embedded in international trade. Nat. Geosci. 9, 111–115.
- Zhang, Q., Jiang, X., Tong, D., Davis, S.J., Zhao, H., Geng, G., Feng, T., Zheng, B., Lu, Z., Streets, D.G., et al. (2017). Transboundary health impacts of transported global air pollution and international trade. Nature 543, 705–709.
- Lin, J., Pan, D., Davis, S.J., Zhang, Q., He, K., Wang, C., Streets, D.G., Wuebbles, D.J., and Guan, D. (2014). China's international trade and air pollution in the United States. Proc. Natl. Acad. Sci. U S A 111, 1736–1741.
- 84. Brooks, M.L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. J. Appl. Ecol. 40, 344–353.
- Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., Baron, J.S., Bobbink, R., Bowman, W.D., Clark, C.M., et al. (2011). Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21, 3049–3082.
- Peters, G.P., Minx, J.C., Weber, C.L., and Edenhofer, O. (2011). Growth in emission transfers via international trade from 1990 to 2008. Proc. Natl. Acad. Sci. U S A 108, 8903–8908.
- Peters, G.P., and Hertwich, E.G. (2008). CO2 embodied in international trade with implications for global climate policy. Environ. Sci. Technol. 42, 1401–1407.
- Hulme, P.E. (2017). Climate change and biological invasions: evidence, expectations, and response options. Biol. Rev. 92, 1297–1313.
- 89. Rahel, F.J., and Olden, J.D. (2008). Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. 22, 521–533.
- Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., and Osman, R.W. (2002). Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proc. Natl. Acad. Sci. U S A 99, 15497–15500.
- Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukat, Z., Bugmann, H., et al. (2009). Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24, 686–693.
- Schmitz, C., Kreidenweis, U., Lotze-Campen, H., Popp, A., Krause, M., Dietrich, J.P., and Müller, C. (2015). Agricultural trade and tropical deforestation: interactions and related policy options. Reg. Environ. Change 15, 1757–1772.
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., and Foley, J.A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. U S A 107, 16732–16737.
- Pendrill, F., Persson, U.M., Godar, J., Kastner, T., Moran, D., Schmidt, S., and Wood, R. (2019). Agricultural and forestry trade drives large share of tropical deforestation emissions. Glob. Environ. Chang. 56, 1–10.
- Kastner, T., Erb, K.H., and Nonhebel, S. (2011). International wood trade and forest change: a global analysis. Glob. Environ. Chang. 21, 947–956.
- Furumo, P.R., and Aide, T.M. (2017). Characterizing commercial oil palm expansion in Latin America: land use change and trade. Environ. Res. Lett. 12, 024008.
- Dawson, W., Burslem, D.F., and Hulme, P.E. (2015). Consistent effects of disturbance and forest edges on the invasion of a continental rain forest by alien plants. Biotropica 47, 27–37.
- Vila, M., and Ibanez, I. (2011). Plant invasions in the landscape. Landsc. Ecol. 26, 461–472.

Review



- 99. Waddell, E.H., Banin, L.F., Fleiss, S., Hill, J.K., Hughes, M., Jelling, A., Yeong, K.L., Ola, B.B., Sailim, A.B., Tangah, J., et al. (2020). Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. Landsc. Ecol. 35, 1891-1906.
- 100. Zenni, R.D., and Ziller, S.R. (2011). An overview of invasive plants in Brazil. Braz. J. Bot. 34, 431-446.
- 101. Gavier-Pizarro, G.I., Radeloff, V.C., Stewart, S.I., Huebner, C.D., and Keuler, N.S. (2010). Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecol. Appl. 20, 1913–1925.
- 102. Seto, K.C., Güneralp, B., and Hutyra, L.R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Natl. Acad. Sci. U S A 109, 16083-16088.
- 103. Tripathi, S. (2020). Do macroeconomic factors promote urbanization? Evidence from BRICS countries. Asia Pac. J. Reg. Sci. https://doi.org/ 10.1007/s41685-020-00179-z.
- 104. Linsky, A.S. (1965). Some generalizations concerning primate cities. Ann. Assoc. Am. Geogr. 55, 506-510.
- 105. Moomaw, R.L., and Shatter, A.M. (1996). Urbanization and economic development: a Bias toward large cities? J. Urban Econ. 40, 13-37.
- 106. Thia, J.P. (2016). Trade and urbanisation. World Econ. 39, 853-872.
- 107. McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247-260.
- 108. Shochat, E., Lerman, S.B., Anderies, J.M., Warren, P.S., Faeth, S.H., and Nilon, C.H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60, 199-208.
- 109. Bulleri, F., and Chapman, M.G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26-35.
- 110. Mineur, F., Cook, E.J., Minchin, D., Bohn, K., MacLeod, A., and Maggs, C.A. (2012). Changing coasts: marine aliens and artificial structures. In Oceanography and Marine Biology: An Annual Review, R.N. Gibson, R.J.A. Atkinson, J.D. M Gordon, and R.N. Hughes, eds. (CRC Press), pp. 189-233.
- 111. Fioramonti, L. (2013). Gross Domestic Problem: The Politics behind the World's Most Powerful Number (Zed Books).
- 112. Hulme, P.E. (2020). One Biosecurity: a unified concept to integrate human, animal, plant, and environmental health. Emerg. Top. Life Sci. 4, 539-549.
- 113. Hulme, P.E. (2021). Advancing One Biosecurity to address the pandemic risks of biological invasions, BioScience, https://doi.org/10.1093/biosci/
- 114. Caley, P., Ingram, R., and De Barro, P. (2015). Entry of exotic insects into Australia: does border interception count match incursion risk? Biol. Invasions 17, 1087-1094.
- 115. Lee, W., Lee, Y., Kim, S., Lee, J.H., Lee, H., Lee, S., and Hong, K.J. (2016). Current status of exotic insect pests in Korea: comparing border

- interception and incursion during 1996-2014. J. Asia Pac. Entomol. 19, 1095-1101.
- 116. Ward, D.F., Beggs, J.R., Clout, M.N., Harris, R.J., and O'Connor, S. (2006). The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. Divers. Distrib. 12, 601-609.
- 117. Eschen, R., Rigaux, L., Sukovata, L., Vettraino, A.M., Marzano, M., and Grégoire, J.C. (2015). Phytosanitary inspection of woody plants for planting at European Union entry points: a practical enquiry. Biol. Invasions 17, 2403-2413.
- 118. Bacon, S.J., Bacher, S., and Aebi, A. (2012). Gaps in border controls are related to quarantine alien insect invasions in Europe. PLoS One 7,
- 119. Katsanevakis, S., Zenetos, A., Belchior, C., and Cardoso, A.C. (2013). Invading European seas: Assessing pathways of introduction of marine aliens. Ocean Coast Manag. 76, 64-74.
- 120. Early, R., Bradley, B.A., Dukes, J.S., Lawler, J.J., Olden, J.D., Blumenthal, D.M., Gonzalez, P., Grosholz, E.D., Ibañez, I., Miller, L.P., et al. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. Nat. Commun. 7, 12485.
- 121. Paini, D.R., Sheppard, A.W., Cook, D.C., De Barro, P.J., Worner, S.P., and Thomas, M.B. (2016). Global threat to agriculture from invasive species. Proc. Natl. Acad. Sci. U S A 113, 7575-7579.
- 122. Liu, X., Blackburn, T.M., Song, T., Li, X., Huang, C., and Li, Y. (2019). Risks of biological invasion on the Belt and road. Curr. Biol. 29, 499-505.
- 123. Sardain, A., Sardain, E., and Leung, B. (2019). Global forecasts of shipping traffic and biological invasions to 2050. Nat. Sustain. 2, 274–282.
- 124. Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., et al. (2011). Socioeconomic legacy yields an invasion debt. Proc. Natl. Acad. Sci. U S A 108, 203-207.
- 125. Bekkers, E., Francois, J.F., and Rojas-Romagosa, H. (2018). Melting ice caps and the economic impact of opening the Northern Sea Route. Econ. J. 128, 1095-1127.
- 126. Ricciardi, A., Blackburn, T.M., Carlton, J.T., Dick, J.T., Hulme, P.E., Iacarella, J.C., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., et al. (2017). Invasion science: a horizon scan of emerging challenges and opportunities. Trends Ecol. Evol. 32, 464-474.
- 127. Lund, S., and Tyson, L. (2018). Globalization is not in retreat: digital technology and the future of trade. Foreign Aff. 97, 130.
- 128. Convention on Biological Diversity (2020). Global Biodiversity Outlook 5 (Secretariat of the Convention on Biological Diversity).
- 129. Gollasch, S., and David, M. (2018). Ballast water management convention implementation challenges. Ocean Yearb. 32, 456-476.
- 130. Cohen, N.J., Slaten, D.D., Marano, N., Tappero, J.W., Wellman, M., Albert, R.J., Hill, V.R., Espey, D., Handzel, T., Henry, A., et al. (2012). Preventing maritime transfer of toxigenic Vibrio cholerae. Emerg. Infect. Dis. 18, 1680-1682.