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Impacts of globalisation on biological invasions

Fenn-Moltu Gyda

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Faculté de biologie
et de médecine

Département d'écologie et évolution

Impacts of globalisation on biological invasions

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

par

Gyda FENN-MOLTU

MSc in Conservation and Biodiversity, University of Exeter

Jury

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Summary

We are in a period of dramatic global changes where human activities are causing massive biodiversity loss, pollution, and climate change. Species are increasingly introduced outside their native range through the globalisation of human economies and societies, occasionally producing invasive species that threaten native ecosystems. Yet the mechanisms behind patterns of biological invasion are not well understood, particularly for organisms that are introduced unintentionally. There is an urgent need to understand the drivers of non-native species dispersal and establishment to inform appropriate policy and management responses. Non-native insects are widespread, diverse, and typically introduced unintentionally, making them an ideal system to study the impacts of globalisation on biological invasions. In the first chapter of this thesis, we assessed insect movements with commodity trade, using nearly two million border interception records from inspections at air, land and maritime ports in six regions. We found that movements of plant and wood products were the main introduction pathway for insects, but a wide variety of commodities were involved. Insects in the same genus tended to share similar commodity associations. In the second chapter we studied factors determining the number of species exchanged between regions based on border interceptions and records of established insects. We found that trade intensity had a significant effect on the number of species being transported and establishing, as did the biogeographic region of origin. Countries with stronger economies supplied more transported species, and more species established when introduced within their native biogeographic region. In chapter three we explored the diversity and host generalism of entomophagous insects arriving in the USA with potential for accidental biological control. We found that natural enemies from 93 different families were intercepted, mainly with plants and plant products. About a third of natural enemy species arrived from more than one country, and two thirds were polyphagous host generalists. In chapter four we assessed the prevalence of asexual reproduction and feeding habits among thrips (order Thysanoptera) at different stages of the invasion process. We found that herbivores were over-represented and fungivores under-represented among non-native thrips. The capacity for asexual reproduction was increasingly common at progressive invasion stages. Together, these studies add to our understanding of human-mediated dispersal and invasion in insects. Targeted research will be essential for effective understanding, legislation, and management of invasive species going forwards.

Résumé

Nous vivons une période de changement global dramatique où les activités humaines sont à l'origine d'une perte massive de biodiversité, de pollution et de changement climatique. Les espèces sont de plus en plus souvent introduites en dehors de leur aire de répartition naturelle par le biais de la mondialisation des économies et des sociétés humaines, produisant parfois des espèces envahissantes qui menacent les écosystèmes indigènes. Pourtant, les mécanismes qui sous-tendent les modèles d'invasion biologique ne sont pas bien compris, en particulier pour les organismes introduits involontairement. Il est urgent de comprendre les moteurs de la dispersion et de l'établissement des espèces non indigènes afin d'éclairer des politiques et des mesures de gestion appropriées. Les insectes non indigènes sont très répandus, diversifiés et généralement introduits involontairement, ce qui en fait un système idéal pour étudier les impacts de la mondialisation sur les invasions biologiques. Dans le premier chapitre de cette thèse, nous avons évalué les mouvements d'insectes dans le cadre du commerce des marchandises, en utilisant près de deux millions d'observations provenant d'inspections frontalières dans les ports aériens, terrestres et maritimes de six régions. Nous avons constaté que les mouvements de produits végétaux et de bois constituaient la principale voie d'introduction des insectes, mais qu'une grande variété de marchandises étaient aussi concernées. Les insectes d'un même genre ont tendance à être associés à des produits similaires. Dans le deuxième chapitre, nous avons étudié les facteurs qui déterminent le nombre d'espèces échangées entre les régions, en nous basant sur des observations aux frontières et des relevés d'établissements d'insectes. Nous avons constaté que l'intensité du commerce avait un effet significatif sur le nombre d'espèces transportées et établies, tout comme la région biogéographique d'origine. Les pays dont l'économie est plus forte fournissent plus d'espèces transportées, et plus d'espèces s'établissent lorsqu'elles sont introduites dans leur région biogéographique d'origine. Dans le troisième chapitre, nous avons étudié la diversité et le caractère généraliste des hôtes des insectes entomophages arrivant aux États-Unis, avec un potentiel de contrôle biologique accidentel. Nous avons constaté que des ennemis naturels de 93 familles différentes ont été interceptés, principalement avec des plantes et des produits végétaux. Environ un tiers des espèces d'ennemis naturels provenaient de plus d'un pays, et deux tiers étaient des généralistes polyphages. Dans le chapitre quatre, nous avons évalué la prévalence de la reproduction asexuée et les habitudes alimentaires des Thysanoptères à différents stades du processus d'invasion. Nous avons constaté que les herbivores étaient

surreprésentés et les mycophages sous-représentés parmi les thrips non indigènes. La capacité de reproduction asexuée était de plus en plus fréquente à des stades d'invasion progressifs. L'ensemble de ces études nous permet de mieux comprendre la dispersion par les activités humaines et les invasions d'insectes. Une recherche ciblée serait essentielle pour une compréhension, une législation et une gestion efficaces des espèces envahissantes à l'avenir.

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Introduction

It is increasingly accepted that we have entered the Anthropocene; a new geological epoch where humans have significantly altered our planet's geology, climate, and ecosystems (Waters *et al.*, 2016). We are living in a period of massive global change where land- and seascapes are increasingly shaped by human activities, often in ways that fuel the triple threat of biodiversity loss, pollution, and climate change. All three of these interlinked crises pose an existential threat to our civilizations (Ceballos, Ehrlich and Raven, 2020).

To help us tease apart the complex global processes that we have triggered, our planet can be considered in terms of different spheres. For example, the lithosphere is the solid, rocky outer part of the Earth, the atmosphere is the layer of gases surrounding the planet, and the biosphere is made up of all the Earth's living organisms. It has been suggested that recently a new sphere has emerged: the technosphere that encompasses all of the technological objects manufactured by humans, humans ourselves, and the professional and social systems by which we interact with technology (Haff, 2013). The technosphere is profoundly changing the biosphere, leading to catastrophic biodiversity loss through local and global extinctions, an overall loss of biomass, and creating biological invasions through the movement of species outside of their native range (IPBES, 2019). Historically, biogeographic barriers such as oceans and mountain ranges have delimited the distribution, dispersal, and evolution of organisms. One of the important markers of the Anthropocene is how human trade and mobility are transferring organisms across these barriers at an ever increasing rate, thereby rearranging patterns of biodiversity at the global scale (Lewis and Maslin, 2015). Entirely novel communities are arising through the human-mediated dispersal of species, leading to complex and often unpredictable consequences.

Biological invasions in a changing world

Biological invasions are today considered one of the main drivers of change in nature (IPBES, 2019). According to a recent report from the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (Roy *et al.*, 2023), over 37,000 species have been introduced outside their native range by human activities to date. More than 3,500 of these species are considered to be invasive with documented negative impacts for nature and human societies.

Such invasive species are often ranked as one of the main global threats to biodiversity (IPBES, 2019). However, the examples used to demonstrate this, such as the introduction of the brown tree snake (*Boiga irregularis,* Squamata: Colubridae) that is thought to have caused the extinction of most native bird species on Guam (Wiles *et al*., 2003), do not happen in isolation. Much of the evidence for the negative impacts of invasive species is based on a correlation between invasive species dominance and native species decline within already degraded habitats (Didham *et al*., 2005). It is often unclear whether the invasive species are themselves causing biodiversity loss, or if their impacts are confounded with other ecosystem changes that are both driving the loss of native species and facilitating invasions (MacDougall and Turkington, 2005). Furthermore, most non-native species are not actually considered invasive. Many non-native species integrate into existing communities without notable negative effects on the native species being observed (Roy *et al*., 2023), and many also have positive impacts on the native species they interact with (e.g., Dick, Etchelecu and Austerlitz, 2003; Schmidt *et al*., 2005; Rodriguez, 2006). Only about 6 % of non-native plants, 14 % of non-native vertebrates, 11 % of non-native microbes and 22 % of non-native invertebrates have documented negative ecological or economic impacts in their introduced range (Roy *et al*., 2023). As most species considered to be invasive are, unsurprisingly, those that affect human economic interests involving agriculture, forestry, infrastructure, and public health, it is likely that the impacts of many other non-native species have as yet gone undocumented. However, the global economic cost of invasive species exceeded 423 billion US dollars annually in 2019 (Roy *et al*., 2023). Non-native species are profoundly altering ecosystems around the world, and certain invasive species are known to have devastating ecological consequences (Roy *et al*., 2023).

Insect invasions as a model system

Insects are among the most expensive and damaging invasive organisms in terrestrial habitats worldwide (Bradshaw *et al*., 2016; Renault *et al*., 2022). They comprise 12 of the "100 worst invasive species" listed by the Invasive Species Specialist Group (Global Invasive Species Database, 2023), and have considerable impacts on agriculture (Sileshi, Gebeyehu and Mafongoya, 2019), forestry (Brockerhoff *et al*., 2010; Aukema *et al*., 2011), infrastructure (Buczkowski and Bertelsmeier, 2017), and public health (Medlock *et al*., 2015; Renault *et al*., 2021), as well as on native ecosystems (Kenis *et al*., 2009; Clark, Skowronski and Hom, 2010;

Wagner and Van Driesche, 2010). Insects are also one of the most taxonomically and functionally diverse groups of organisms on Earth (Wilson, 1987; Stork, 2018), and occupy almost every terrestrial habitat, so it is perhaps unsurprising that they have become such successful non-native organisms.

Insects provide key ecosystem functions such as predation, nutrient cycling, and pollination to the communities they inhabit (Dangles and Casas, 2019). This implies considerable potential for ecological impacts when insect species enter a new community that they have not co-evolved with. Non-native insects influence ecosystems both through relatively simple trophic interactions such as predation, herbivory, or parasitism, and through more complex interactions like competition for food and habitat resources, apparent competition as prey of the same predators, transmission of pathogens, and pollination disruption (Kenis *et al.*, 2009). Certain invasive insects can also have cascading effects on ecosystem processes (e.g., Ryan, Ortmann and Herian, 2014; Kehoe, Frago and Sanders, 2021). Such cascading effects can occur because species are connected through a complex network of interactions, meaning that an initial extinction triggered by an invasive species can generate a series of secondary extinctions within the community.

Despite their ecological importance, invasions of small organisms like insects and mites have not been as intensively studied as some other taxa (Pyšek *et al.*, 2008; Kenis *et al.*, 2009; Jeschke *et al.*, 2012). Yet due to the economic and societal costs associated with insect introductions, they have become a key target for biosecurity efforts worldwide. Notably, unlike many non-native plants and vertebrates that are carefully selected and introduced to fulfil human interests, most insect introductions occur accidentally (Hulme *et al.*, 2008). While there are insect species that have been introduced intentionally as biological control agents for pest management (Hajek and Eilenberg, 2018), as food, or through the pet trade (Kumschick *et al.*, 2016), the majority are transported without direct human intent or supervision. Along with their impressive diversity and global prevalence, this makes insect introductions an excellent system to study the relationship between human activities and biological invasions.

Stages of the invasion process

We can consider the invasion process as a series of sequential stages that a species must pass through to successfully establish and spread, each separated by various biotic and abiotic barriers (Blackburn *et al*., 2011; Schulz, Lucardi and Marsico, 2021). The process starts with an initial dispersal event where individuals become associated with a commodity or transport vector, or are intentionally captured for transport. This is followed by a transport stage where species are moved outside their native range by a vector, often cars, trains, boats, or airplanes. Upon arrival, the surviving individuals are introduced to a new area, either by detaching from the commodities or transport vector they were transported with, by escaping captivity, or by being deliberately released. Those that find suitable conditions where they are introduced may establish a self-sustaining population there, and subsequently may spread further and potentially cause impacts in their non-native range (Blackburn *et al*., 2011; Gippet *et al*., 2019; Figure 1). Each of these temporal phases uniquely affects the dynamics and geography of an invasion. Separating the stages in this way helps us to identify characteristics of the human activities that are key drivers of each stage, facilitates understanding of how species are filtered based on their traits throughout the process, and can provide a support for predicting invasion risk and allocating resources for managing invasions.

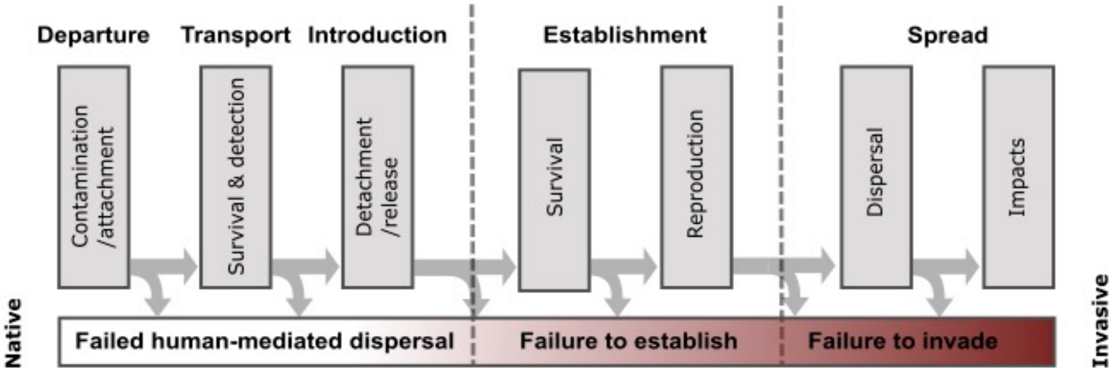

Figure 1. Stages of the invasion process, adapted from the framework proposed by Blackburn *et al*. (2011). The grey boxes indicate barriers separating the stages along a spatial and temporal gradient from native to invasive.

Introduction pathways

Managing the negative impacts of an invasion becomes increasingly difficult as the invading population spreads and grows (Leung *et al*., 2002; Venette *et al*., 2021; Figure 2). Knowledge of the specific pathways that insects are spread through is therefore crucial for implementing effective prevention methods early on, including trade regulations, interception programmes, screening systems and early warning strategies (Hulme, 2006). The manner by which human activities drive the different stages of the dispersal process also depends on the particular pathway through which a species is dispersed (Pergl *et al*., 2017).

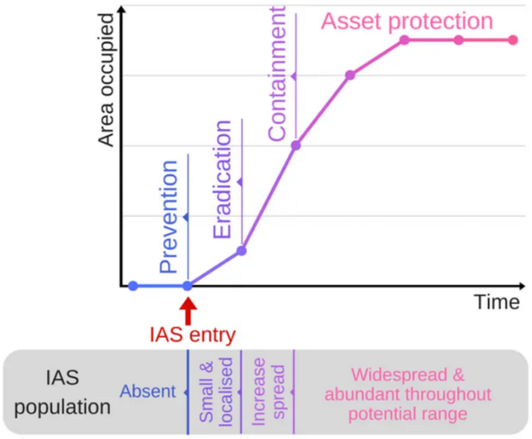

Figure 2. Management options for invasive species as a factor of their spread and time since introduction (IUCN, 2021), adapted from the Invasive Plants and Animals Policy Framework, State of Victoria Department of Primary Industries, (2010). IAS refers to Invasive Alien Species, see Table 1 for definitions of ‘invasive’ and ‘alien’.

There have been considerable efforts into classifying the introduction pathways of non-native species, with a unified framework proposed by Blackburn *et al*. (2011). In this framework, non-native species can arrive and enter a new region through three broad mechanisms, resulting in six principal pathways: importation of a commodity (the release, escape, and transport-contaminant pathways), arrival of a transport vector (the transport-stowaway pathway), or spread from a neighbouring region (the corridor, and unaided pathways) (Convention on Biological Diversity, 2014). Figure 3 illustrates the contaminant pathway, the hitchhiking (or stowaway) pathway, and the harvesting (or release/escape) pathways across the three first temporal phases of the invasion process, ending with species introduction to a new area.

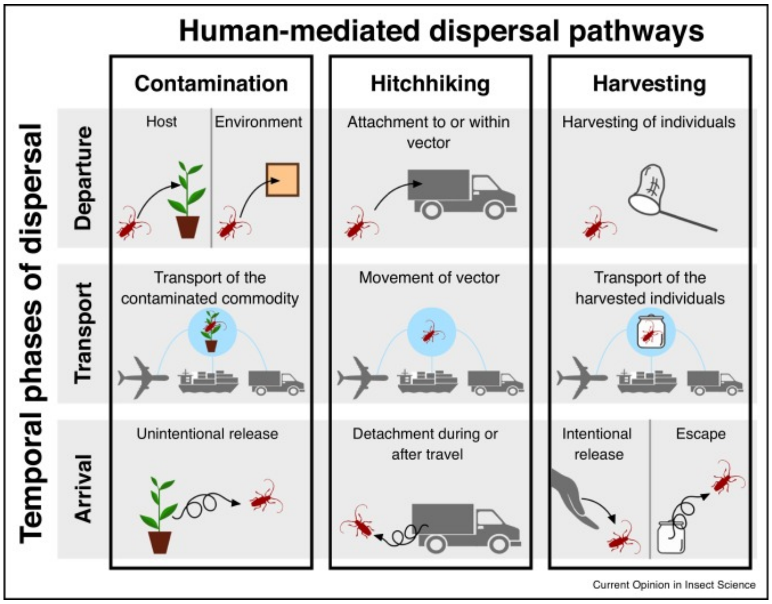

Figure 3. Human-mediated dispersal can be divided into three phases: departure, transport, and arrival, here illustrated for different insect invasion pathways. Figure from Gippet *et al*. (2019). The contamination and hitchhiking pathways are unintentional. In the harvesting pathway species are intentionally captured and transported, but arrival can be either intentional (release) or unintentional (escape).

One of the main determinants of establishment success is propagule pressure: a composite measure of the number of individuals introduced to an area (propagule size) and the number of separate introduction events (propagule number) (Lockwood, Cassey and Blackburn, 2005; Colautti, Grigorovich and MacIsaac, 2006). The more individuals of a species that are introduced to an area, the more likely this species is to establish. Similarly, the more different species that are introduced to an area, known as colonization pressure, the more species can be expected to subsequently establish there (Lockwood, Cassey and Blackburn, 2009; Blackburn, Cassey and Duncan, 2020). As the title of Lockwood *et al*.'s 2009 paper succinctly puts it: "the more you introduce the more you get".

Globalisation and rising introduction rates

Although humans have been transporting species outside their native ranges for millennia, introductions are now happening at an unprecedented rate as our global society becomes increasingly interconnected (Ricciardi, 2007; Seebens *et al*., 2017). Globalisation is the process of interaction and integration among people, companies, and governments worldwide (James and Steger, 2014). While it is primarily an economic process, globalisation is also associated with exchanges of information, ideas, beliefs and culture. More recent advances in transportation and telecommunication infrastructure, such as shipping containers, smartphones and the internet, have strongly accelerated the growing interdependence of economic and cultural activities around the world. While species can arrive to new regions directly through human travel and migration (for example, *Aedes albopictus* (Culicidae: Diptera) spreading in cars, Eritja *et al.*, 2017), trade is widely regarded as the primary driver of invasions in both terrestrial and aquatic ecosystems (Jenkins, 1996; Hulme, 2009). International trade occurs due to geographical specialisation in either natural resources or the production of goods, with buyers and sellers located in different countries. The resulting exchange of commodities between regions offers ample opportunities for insects to be transported, either as contaminants of the traded commodity, or as hitchhikers with the transport vector itself (Figure 3). The evolution of increasingly short travel times may also mean that surviving transport is less of a barrier than it has been in the past (Kobelt and Nentwig, 2008; Hulme, 2021).

The precise routes, ports, transportation time, type, and volume of trade and travel varies depending on the transport vector in question. Figure 4 shows the global network of shipping and aviation routes that tightly link geographically distant parts of the world. In 2021, over 80 % of the global trade volume was carried by sea (UNCTAD, 2022). Since the introduction of shipping containers in the 1960s, huge container ships operate worldwide between hub ports built for rapid onwards transfer of cargo to road, rail and canal transport. In 2020, the global container port throughput equalled 815 million TEUs (twenty-foot equivalent units, representing the dimensions of a 20 foot standardized shipping container) (UNCTAD, 2022). Simultaneously, the aviation industry has expanded rapidly, with 4.46 billion air passengers in 2019 (prior to the Covid-19 pandemic) (World Bank Group, 2023). While air freight makes up a small proportion of global trade, flights may be an important source of insect introductions nonetheless (73 % of plant pest interceptions in the USA from 1984-2000 occurred at airports, according to McCullough *et al.*, 2006). Airports are also more numerous than maritime ports, and allow for greater penetration into continental regions (Hulme, 2009).

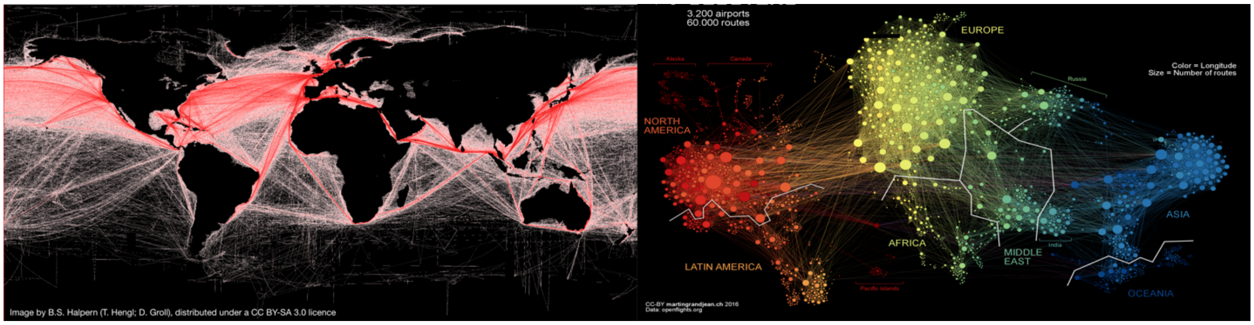

Figure 4. Global shipping and aviation routes illustrate the wide-reaching exchanges between geographically distant regions. The map to the left shows the relative density of commercial shipping routes, while the map to the right shows routes of global air traffic.

Globalisation has not been a linear process, however. There have been several distinct "waves" of globalisation characterised by step-changes in trade and global integration, but there is little consensus on how these waves are to be delimited. Baldwin and Martin (1999), and Federico and Tena-Junguito (2017) for instance, define a first wave from around 1820 to 1914 and a second wave from 1960 onwards, Collier and Dollar (2002) refer to three waves from 1870 to 1914, 1945 to 1980, and 1980 to the present, and the World Economic Forum suggests that we have now recently entered "globalisation 4.0" (Vanham, 2019). There is as yet no standard measurement for globalisation in use, nor indeed a universally accepted definition (Samimi, Lim and Buang, 2011). Single indicators, often reflecting trade openness, are frequently used as a proxy (Gygli *et al*., 2019), while more complex measures such as the KOF Globalisation Index (Gygli *et al*., 2019) or the New Globalisation Index (NGI) (Vujakovic, 2010) have been proposed. Overall, it seems that the rate of species introductions is shaped by the varying intensity of global exchanges over time (Bertelsmeier *et al*., 2017; Bonnamour, Gippet and Bertelsmeier, 2021).

Biosecurity efforts and border inspections

Attempts to limit introductions of non-native species through trade have a long history, with quarantine and inspection services to protect agricultural crops established as early as 1899 in the Netherlands, 1902 in Australia, and 1912 in the United States (Hulme, 2014). There is a particular focus on herbivorous insects, for example, the International Plant Protection Convention was created to regulate the global spread and introduction of plant pests (i.e., organisms that are harmful to plants) (IPPC, 2023). Similarly, risk assessments for invertebrates are usually carried out by the phytosanitary sector (e.g., USDA-APHIS, 2000). Controlling the movements and initial entry of a non-native species is generally considered to be more cost-effective than control or eradication programmes later on (Convention on Biological Diversity, 2002) (Figure 2). Thus, it is increasingly recognized that biosecurity efforts should primarily focus on preventing the initial entry of non-native species (Lockwood, Cassey and Blackburn, 2009; Simberloff *et al*., 2013). Biosecurity efforts here refer to the research, procedures and policies that deal with the exclusion, eradication, or management of the risks posed by the introduction of plant and animal pests, pathogens, genetically modified organisms, and non-native species (Beale *et al*., 2008). While our ability to identify future invasive species is largely based on their prior invasion history, a large proportion of the species introduced in recent years have never previously been recorded outside their native range (Seebens *et al.,* 2018). These 'emerging' non-native species represent a significant challenge for biosecurity interventions, warranting a shift towards risk assessment approaches that rely less on invasion history.

As part of national biosecurity programmes, many countries inspect a proportion of the goods, mail, and personal baggage arriving at their land borders, air- and seaports, and transitional facilities (Saccaggi *et al*., 2016; Black and Bartlett, 2020). It is only possible to inspect a small fraction of imports due to the huge volume of trade being received (Natural Research Council, 2002), so border inspections are not typically a primary method for excluding non-native species. Yet such inspections play an important role in monitoring the presence of organisms across various introduction pathways. This information is central to identifying invasion risks, defining phytosanitary policies (e.g., import bans and mandatory phytosanitary treatments) and monitoring compliance with existing import regulations (Sequeira and Griffin, 2014; IPPC Secretariat, 2021). Accordingly, border interception records can provide a valuable insight into the otherwise largely unobserved movement of insects through human-mediated dispersal (Turner *et al*., 2021).

In this thesis we have used interception records from nine countries or regions to assess the unintentional transport of insects around the world. Most research on the human-mediated dispersal of insects so far has dealt with specific taxa or feeding groups arriving in a single country, often on a pre-selected suite of traded commodities. However, non-native species do not respect political boundaries. Identifying general trends that apply across regions and insect groups would thus be beneficial for biosecurity efforts in a broader range of countries with varying resources available for managing invasions. In chapter one we used records of the commodity types that insects were detected with during border inspections in Australia, New Zealand, Europe, Japan, the United States of America, and Canada to identify key introduction pathways that are relevant across taxa and geographical regions.

However, countries vary significantly in their sampling methods, identification abilities, and the species and commodities that they preferentially target (Whattam *et al.*, 2014; Turner *et al.*, 2021). These limitations apply to the interception records analysed in this thesis, making the variation between regions, and over time, a substantial, if largely unavoidable, source of bias. For instance, the European and Mediterranean Plant Protection Organization (EPPO) is responsible for cooperation and harmonization in plant protection within the Euro-Mediterranean region (EPPO, 2023). Economically harmful plant pests are banned from entering and being moved around Europe, and interceptions are largely restricted to these quarantine species (European Commission, 2002). Moreover, the sampling efforts vary significantly between EPPO member states (Bacon, Bacher and Aebi, 2012). Conversely, in Australia and New Zealand, strict biosecurity programmes rather operate based on “positive lists” of species that have been assessed and are considered to be unproblematic (Eschen *et al.*, 2015). The United States, Canada, South Africa and Japan also apply “negative lists” of actionable quarantine pests (Animal and Plant Health Inspection Service, 2020; Canadian Food Inspection Agency, 2021; Ministry of Agriculture and Fisheries, 2021), but these measures are generally more restrictive than in Europe. Despite the rigorous measures in place, Work *et al.* (2005) estimated that even statistically sound inspection methods such as the USDA-APHIS AQIM protocol probably only detect 19-50 % of the insect species arriving, depending on the pathway. Nevertheless, combining border interception data from different sources can provide valuable information on global flows of insects between regions, as well as the introduction pathways and types of commerce involved in insect introductions. Data with regional differences can provide a more comprehensive picture of the global trends in human-mediated dispersal of insects when considered together.

Long-term monitoring efforts at large spatial scales can substantially increase the accuracy and rate at which non-native species are detected (Haubrock *et al.*, 2023). The interception records analysed in this thesis span five continents and several decades, thereby illustrating patterns of species exchanges across time and space. The information on species' identity, origins, and introduction pathways uncovered in these data is highly informative both for improving our understanding of the human-mediated dispersal of insects, and for the management of insect invasions globally. In chapter two we combined interception records from Canada, mainland USA, Hawaii, Japan, Australia, New Zealand, Great Britain, South Korea and South Africa with comprehensive lists of non-native insects established in these regions to disentangle the processes occurring during the transport and establishment stages. We linked border interceptions with historical trade records, and investigated the influence of biogeography, socio-economic variables, and biosecurity regulations on the species richness exchanged between world regions.

Non-native species that have already established in a country may continue to spread over time, either by expanding their range within the region or subsequently being transported to new regions through a process known as the 'bridgehead effect' (Lombaert *et al.*, 2010; Bertelsmeier and Keller, 2018; Bertelsmeier *et al.*, 2018). Moreover, the capacity and incentive of countries to prevent insect invasions varies considerably (Early *et al.*, 2016; Faulkner, Robertson and Wilson, 2020). To address this at a global level, a number of international agreements have been instituted and international standards have been set to prevent the transportation of invasive species (McGeoch *et al.*, 2010; Brenton-Rule, Barbieri and Lester, 2016; Turbelin, Malamud and Francis, 2017). There has been progress in implementing specific biosecurity practices, such as the harmonized international standard ISPM-15 specifying phytosanitary treatments for wood packaging, that have likely reduced rates of insect introductions (Haack *et al.*, 2014). A less favourable aspect of this progress are the barriers to economic advancement in developing countries when invasive insects present demonstrable phytosanitary concerns that prevent or curtail international trade in the plant-based commodities that are exported from those countries (Hulme, 2021).

The traits of a successful invasive species

Each stage of the invasion process can be seen as an ecological filter that species must pass through before progressing to the next one (Richardson *et al*., 2000; Mitchell *et al*., 2006). Each stage has its own dynamics, depends on different factors (Lockwood *et al.,* 2005), and will favour different sets of biological traits. Searching for traits that predict invasiveness has been one of the most common lines of research in invasion biology since Baker (1965) listed the traits of the "ideal weed". Yet the results have been rather idiosyncratic (Pyšek and Richardson, 2007). Some of the traits most frequently suggested to promote invasion success are those favouring rapid reproduction, good dispersal ability, and a generalist diet (e.g., Kolar and Lodge, 2001; Pyšek and Richardson, 2007; Hayes and Barry, 2008; Peacock and Worner, 2008). For insects specifically, traits linked to life history, habitat use, and feeding niche have been implicated. For example, sap feeders and detritivores were dominant among non-native insects in Austria and Switzerland (Kenis *et al*., 2007) and ground nesting ants were more likely to become established in the USA compared to arboreal species (Suarez, Holway and Ward, 2005). Non-native eucalypt specialists had longer flight seasons, smaller body size, closer host-associations, lower incidence of diapause, and more generations per year than natives (Nahrung and Swain, 2015). Moreover, reproductive mode has been implicated in invasion success for both insects and other taxa. For instance, ant invasions seem to be linked to polygyny and the ability to form supercolonies (Eyer and Vargo, 2021). Parthenogenesis in particular, whether obligate or facultative, allows insects to quickly exploit new resources while avoiding the constraint of finding mates (Lattin and Oman, 1983). This would have clear benefits for a species arriving in a new area, and has been suggested to be an important mechanism in the establishment of non-native Thysanoptera (Morse and Hoddle, 2006), Scolytinae (Coleoptera) (Lantschner, Corley and Liebhold, 2020) and Hymenoptera (Queffelec *et al*., 2021).

However, identifying traits that are consistently linked to invasion success has met with difficulties. This may in part be due to a confounding relationship with propagule pressure for many of the traits considered (Lockwood, Cassey and Blackburn, 2005). Cassey *et al*. (2004) for example, found that propagule pressure was correlated with many of the variables previously thought to influence establishment success in birds, leaving habitat generalism as the only trait relevant for establishment success in their review. These difficulties have been further compounded by a lack of information on the stages of the invasion process occurring prior to establishment and spread. While it has been possible to control for the introduction stage in rare cases where release attempts have been well-recorded (birds: Blackburn, Cassey and Lockwood, 2008; Chiron, Shirley and Kark, 2009; mammals: Jeschke and Geùnovesi, 2011), isolating the factors driving success at each stage has rarely been accessible while studying patterns of unintentional invasions (Puth and Post, 2005). Many families with a high proportion of non-native species share traits that encourage intentional introductions based on human preferences (plants: Pyšek, 1998; birds: Lockwood, 1999), and it is likely that there are similarly specific traits that facilitate unintentional transport. These traits may differ from those promoting successful establishment later on (Gippet *et al*., 2019), which are likely to be highly context-dependent (Daehler, 2003). The differences in selection pressure throughout the invasion process highlight the importance of accounting for the ecological filters acting at each sequential stage.

Both international and national biosecurity efforts mainly target introductions of herbivorous insects (Magarey, Colunga-Garcia and Fieselmann, 2009), and to some extent hematophagous insects (Cuthbert *et al*., 2023), with less attention given to preventing the spread of insects with other feeding habits. In chapter three we used border interceptions and records of established non-native insects in the United States to explore the unintentional movement of insect predators and parasitoids through international trade. We assessed the number and diversity of 'natural enemy' insect families that arrived at the US border, and we quantified the host diversity, invasion status, and commodity associations for the species that were detected. In chapter four we used non-native thrips (order Thysanoptera) as a model taxon to analyse the importance of certain traits for invasion success at different invasion stages. Thysanoptera are overrepresented among non-native insect assemblages (Liebhold *et al*., 2016), and include a number of widespread and invasive agricultural pests (e.g., *Frankliniella occidentalis, Thrips tabaci,* and *Thrips palmi*, Cannon, Matthews and Collins, 2007; Zhao *et al*., 2017). We used records of intercepted thrips species along with lists of established thrips to assess the importance of feeding guild, host plant diversity, and the capacity for asexual reproduction for successfully passing through the transport and establishment stages of the invasion process.

Etymology and terminology in invasion science

As our world changes, our ability to describe, understand and adapt to the processes occurring is founded on effective communication. With regards to invasion science, this is hindered by the field having evolved and expanded rapidly without a standardized framework for the technical terms being used. Almost thirty years ago, Pyšek (1995) found that studies on biological invasions recurrently used the term 'invasive' and its derivatives without explicitly defining it, noting at least 13 different uses in the literature. A similar issue has been noted for terms such as 'naturalized' (Richardson *et al*., 2000), or 'propagule pressure' (Lockwood, Cassey and Blackburn, 2009). Furthermore, the terminology applied also varies considerably depending on the study taxon, location and specific field of research. For example in botany, species that were introduced in recent history (specifically after 1492 in the UK) are termed 'neophytes' (Preston, Pearman and Hall, 2004), while this term is not generally applied in studies of other introduced taxa. The inconsistent and unclear vocabulary in use can limit communication and collaboration in research and management of non-native species (Almena *et al*., 2023). For example, Castro *et al*. (2023) found that the ambiguous terminology used in invasion science hinders effective reporting of non-native taxa for regional checklists.

To further complicate the situation, many species are shifting their ranges in response to changing environmental and climatic conditions, thereby arriving in areas outside their native range without direct human intervention (Parmesan *et al*., 1999; Lenoir and Svenning, 2015). The classification of such range-expanding species as native, non-native, or as a separate 'neonative' category is still debated, but has important implications for environmental legislation and biodiversity management (Essl *et al*., 2019). Unsurprisingly, the definition of what is a native species is not straightforward either. What we refer to as native species, or what is considered a species' native range is based on their historical presence in an area. But species' distributions are dynamic, and have shifted considerably in response to changing climates, land use and species interactions throughout history (Beyer and Manica, 2020). Besides, as the human-mediated dispersal of species has been occurring for millennia, it blurs the definition of what can be considered as historically present in an area. Since the Late Pleistocene, between ~129,000 and ~11,700 years ago, human activities have been altering the distributions of a vast array of species, and thereby creating novel communities around the world (Boivin *et al*., 2016).

For instance, already ~20-23 thousand years ago the northern common cuscus (*Phalanger orientalis,* Diprotodontia: Phalangeridae) was intentionally introduced from New Guinea to eastern Indonesia, the Solomon Islands, and the Bismarck Archipelago as a subsistence species (Heinsohn, 2010). Nonetheless, it is important to bear in mind that, analogous to the current extreme rate of extinctions and climate change, recent human activities have dramatically increased the rate, scale, and impact of biological invasions (Ricciardi, 2007).

Lastly, invasion science often relies heavily on military language (Janovsky and Larson, 2019) (the word "invasion" itself is a military term), which can have consequences for how we interpret and communicate research findings. Framing non-native species as inherently threatening to native ecosystems simply by virtue of being "foreign" has the potential to generate discussion and engagement when used in science communication, but can also lead to a discourse that is xenophobic or discriminatory. Using language that is often both politically and emotionally charged can influence how we perceive species introductions, and thereby hinder rational, evidence-based discussion. Shifting towards the use of more precise, clearly defined, and neutral terms, for example consistently using 'non-native' instead of 'exotic' or 'alien' species (Lepczyk, 2022), can help us to communicate in a clearer and more inclusive manner. While there have been several attempts to address the complex terminology in invasion science (reviewed in Almena *et al*., 2023), a general consensus is still lacking. In this thesis I have used the terminology outlined below in Table 1, aiming to be as precise and accurate as possible while applying terms that are widely accepted in the literature.

Table 1: Some of the terminology relating to invasion science, particularly those with multiple or imprecise definitions, the definitions I have used in this thesis, and a non-exhaustive list of synonyms used in the literature.

Term	Definition	Synonyms
Biocontrol	A pest control method involving an agent that is a natural enemy of the target pest (Heutte and Bella 2003). This includes augmentation biological control (Collier and Van Steenwyk, 2004), conservation biological control (Begg *et al*., 2017), and importation biological control. Importation, or classical, biocontrol is the intentional introduction of natural enemies, most often	Biological control

	parasitoids against insect pests and herbivorous insects against plants, to suppress non-native pest and weed populations (Heimpel and Mills, 2017).	
Biogeographic region	The broadest biogeographic division of the Earth's land surface, based on distribution patterns of terrestrial organisms characterized by their evolutionary history within a region. Biogeographic regions are here delimited according to the zoogeographic realms identified by Holt *et al*. (2013), with the large Palearctic region divided into the Eastern and Western Palearctic.	Biogeographic realm
Bridgehead effect	The process where invasive populations are the source of additional secondary introductions (rather than introductions arriving directly from the native range), thereby creating a positive feedback loop (Lombaert *et al*., 2010).	
Colonization pressure	The number of species introduced to an area (Lockwood, Cassey and Blackburn, 2009; Blackburn, Cassey and Duncan, 2020).	Introduction effort
Contaminant pathway	The unintentional movement of live organisms as contaminants of a commodity that is intentionally transferred through international trade, development assistance, or emergency relief (Convention on Biological Diversity, 2014). Contamination occurs because the commodity is the species natural host or part of its immediate environment (Gippet *et al*., 2019).	
Impact	Refers to ecological, economic or social impacts of a non-native species. Ecological impacts are measurable changes to the properties of an ecosystem by a non-native species, which can be positive or negative, and vary in magnitude on a continuous scale (Ricciardi *et al*., 2013). Socio-economic impacts are the costs or benefits associated with a non-native species, including changes to ecosystem services, food production, and management required. Socio-economic costs are strongly dependant on stakeholder perceptions (García-Llorente *et al*., 2008; Pyšek and Richardson, 2010).	Environmental impact, ecological impact, economic impact, social impact, cost, benefit
Established	A species that has established a self-sustaining population outside of their native range following HMD. Here this excludes species that have established indoors	Naturalized

	only, and established species that have subsequently been eradicated.	
Harvesting pathway	The intentional capture of species by humans for some, often commercial, purpose (e.g., the pet trade, biological control) which leads to introductions either by intentional release or subsequent escape from captivity (Gippet *et al*., 2019).	
Hitchhiking pathway	The moving of live organisms attached to transporting vessels and associated equipment and media (Convention on Biological Diversity, 2014). Hitchhiking occurs when individuals actively attach to an object not directly related to their natural environment (Gippet *et al*., 2019).	Stowaway pathway
Human-mediated dispersal (HMD)	The movement of an individual, species or population outside of its native range through human activities. HMD can be either intentional (e.g., species that are transported for horticulture, the pet trade, or for consumption), or unintentional, where species are transported as hitchhikers or contaminants of commodities.	Human-mediated transport, transport
Introduction	The deliberate or accidental release, into the environment of a given territory, of an organism belonging to a non-native taxon (species or lower taxa that has not been observed as a naturally occurring and self-sustaining population in this territory in historical times) (Bern Convention, 1997).	Release, arrival, entry
Introduction pathway	Any means that allows the entry or spread of a pest [or non-native organism], where a pest is any species, strain or biotype of plant, animal or pathogenic agent injurious to plants or plant products (International Plant Protection Convention, 2016). Introduction pathways encompass the suite of processes that transport a species from one location to another, including both the vector and the human activity resulting in an introduction (Genovesi, Shine and Europe, 2004; Pyšek, Jarošík and Pergl, 2011).	Invasion pathway
Invasive	A species or population that has established outside their native range and that has documented negative ecological or economic impacts there. This definition is largely in accordance with that of the Convention on	Pest (animals), weed (plants), harmful, injurious,

	Biological Diversity, namely "an alien species whose introduction and/or spread threatens biological diversity". While invasive has frequently been used as a synonym for non-native, or to refer to species that have spread widely since their introduction in the literature, this usage does not allow for a distinction between established non-native species that negatively impact invaded ecosystems and those that do not have documented negative impacts in their introduced range.	damaging, noxious
Invasion success	The ability of an individual, species or population to successfully pass through the sequential biotic and abiotic barriers throughout the invasion process (for example, an established species has greater invasion success than a species that is transported but does not successfully establish).	
Native	A species, subspecies, or lower taxon, occurring within its natural range (past or present) and dispersal potential (i.e., within the range it occupies historically, or could occupy without direct or indirect introduction or care by humans) (IUCN, 2000).	Indigenous, natural
Native range	The biogeographical area where a species' occurrence has been determined solely by natural evolutionary processes (Almena *et al*., 2023).	Natural range, historical range
Non-native	A species occurring in an area outside of its historically known natural range as a result of intentional or accidental dispersal by human activities (UNEP, 1995). Alien is used in chapter 1.	Alien, exotic, introduced, neophyte, non-indigenous, foreign, adventive
Non-native range	The area where a species is present due to intentional or unintentional human intervention, and where it has not naturally evolved (McNeill, 2003).	Introduced range, new range
Nuisance	Individuals or populations of a native species that cause economic or environmental harm (Iannone *et al*., 2021). Native species cannot be invasive as they have not been introduced by human activities.	Invasive, native invasive
Propagule pressure	A composite measure of the number of individuals released into a region to which they are not native (Carlton, 1996). It incorporates estimates of the absolute number of individuals involved in any one release event	Introduction effort

	(propagule size) and the number of discrete release events (propagule number) (Williamson, 1996; Lockwood, Cassey and Blackburn, 2005).	
Transport	The movement of an individual, species or population outside of its native range through human-mediated dispersal. Transported species includes species intercepted during border inspections, which are destroyed and not subsequently introduced.	Movement, dispersal, human-mediated dispersal

Thesis outline

The main objective of this thesis is to investigate global patterns of insect invasions through human-mediated dispersal. Our understanding of unintentional species introductions is generally based on successfully established species alone, and is therefore limited by the lack of information on earlier stages of the invasion process. In this thesis we use a unique dataset of border interception records from eight different world regions and spanning over a century to analyse trends in the international transport of insect species through trade and travel. We use these interception records to identify major introduction pathways that are relevant across insect taxa and geographical regions. We combine interception records describing the transport stage with comprehensive lists of established non-native insects from the same regions, allowing us to explore key mechanisms acting at different stages of the invasion process. We quantify the diversity of insects from different taxa and feeding guilds that are transported around the world, and analyse the importance of species traits, socio-economic variables, biogeography and trade intensity for insect invasions. The thesis is divided into four chapters.

Contribution to the chapters

I contributed to the curation and cleaning of the border interception data used in all four chapters, and I assigned the harmonized codes to the traded commodities recorded. I contributed to the experimental design for all chapters, and I took the lead on the statistical analysis. I collected and curated the additional data used in chapters 2-4. I contributed to the interpretation of the results for all chapters, and I took the lead on the writing of each chapter.

Chapter 1: Alien insect dispersal mediated by the global movement of commodities

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Author contributions: AML, CB, DSP, GFM, HN, RMT and TY developed the initial idea. AML, DSP, HN, RMT, and TY curated and provided access to the interception records. GFM assigned commodity codes, and analysed the data with support from SO and CB. All authors contributed to the design, discussed the results, and contributed to the writing of the manuscript.

Abstract

Globalisation and economic growth are recognized as key drivers of biological invasions. Alien species have become a feature of almost every biological community worldwide, and rates of new introductions continue to rise as the movement of people and goods accelerates. Insects are among the most numerous and problematic alien organisms, and are mainly introduced unintentionally with imported cargo or arriving passengers. However, the processes occurring prior to insect introductions remain poorly understood. We used a unique dataset of 1,902,392 border interception records from inspections at air, land and maritime ports in Australia, New Zealand, Europe, Japan, the United States of America and Canada to identify key commodities associated with insect movement through trade and travel. A total of 8,939 species were intercepted, and commodity association data were available for 1,242 species recorded between 1960 and 2019. We used rarefaction and extrapolation methods to estimate the total species richness and diversity associated with different commodity types. Plant and wood products were the main commodities associated with insect movement across cargo, passenger baggage and international mail. Furthermore, certain species were mainly associated with specific commodities within these, and other broad categories. More closely related species tended to share similar commodity associations, but this occurred largely at the genus level rather than within orders or families. These similarities within genera can potentially inform pathway management of new alien species. Combining interception records across regions provides a unique window into the unintentional movement of insects, and provides valuable information on establishment risks associated with different commodity types and pathways.

Key words: *Commodity trade, globalization, human-mediated dispersal, insects, introduction pathways, invasion risk*

Introduction

The globalization of human activities facilitates species dispersal across historical biogeographic barriers, such that alien species are now an established part of almost every biological community worldwide (Convention on Biological Diversity, 2001). As the international movement of people and goods accelerates and expands, the rate of new introductions continues to rise (Levine and D’Antonio, 2003; Seebens *et al.*, 2017). Some species that are introduced and overcome biotic and abiotic barriers to establishment (Blackburn *et al.*, 2011) cause harmful ecological or economic impacts in their new range (Pagad *et al.*, 2015). In terrestrial ecosystems, insects are among the most numerous and problematic alien organisms, costing at least 70 billion US$ per year globally (Bradshaw *et al.*, 2016; Diagne *et al.*, 2021). Unlike most alien vertebrates and plants, insects are usually introduced unintentionally (Rabitsch, 2010). This typically occurs through the transport of commodities, either because the commodity is their natural host or their immediate environment (contaminant pathway), or because insects have actively attached to an object not directly related to their natural environment (hitchhiking pathway) (Gippet *et al.*, 2019). Introduction pathways encompass the suite of processes that transport a species from one location to another, including both the vector and the human activity resulting in an introduction (Genovesi and Shine, 2004; Pyšek *et al.*, 2011).

Managing introduction pathways and corresponding commodities is therefore a potentially powerful strategy for preventing new introductions, and thus reducing negative impacts on biodiversity**,** human health (Pyšek and Richardson, 2010; Mazza *et al.*, 2014; Pratt, *et al.*, 2017) and economies (Bradshaw *et al.*, 2016). Risk assessment strategies for alien species often prioritize identifying sources and pathways of introduction (Hulme *et al.*, 2008). Yet when assessing establishment risks and mitigation measures, it may be more efficient to consider the size and composition of species pools moved along particular pathways, rather than focusing on individual species (Brockerhoff *et al.,* 2014). The greater the number of species introduced to a location (colonization pressure), the more species we should expect to establish self-sustaining populations there (Lockwood *et al.*, 2009; Blackburn *et al.*, 2020). Similarly, the number of species transported via a given pathway or commodity is likely closely related to the introduction risk associated with such movement. While progress has been made towards understanding human-mediated dispersal of certain taxa (for example Suarez *et* al., 2005**;** Brockerhoff *et al.*, 2006; Ward *et al.*, 2006; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019), a global analysis of unintentional insect introduction pathways is lacking. Identifying commerce that transports a wide range of insects worldwide would improve our ability to monitor and manage key pathways, particularly in regions with fewer resources available.

The exact pathways responsible for historical species introductions are usually unknown, but alien species databases and inventories often assign species to the most likely pathway based on their ecology and the assumptions of the assessor (Kenis *et al.*, 2007; Essl *et al.*, 2015; Pergl *et al.*, 2017). However, many countries perform inspections of trade goods, mail and personal baggage at ports of entry (i.e., land borders, air and sea ports and transitional facilities) as part of national biosecurity programmes (Saccaggi *et al.*, 2016; Black and Bartlett, 2020). Due to the large volume of trade, it is only possible to inspect a small fraction of imports (Natural Research Council, 2002). Therefore, inspections are typically not a primary method for excluding arrivals of potential pest species. However, inspection plays a key role in national biosecurity programs as a method for monitoring the presence of organisms in various pathways. This information is of great value in identifying invasion risks, setting phytosanitary policies (e.g. import bans and mandatory phytosanitary treatments) and monitoring compliance with existing import regulations (Sequeira and Griffin, 2014; IPPC Secretariat, 2021). Countries vary in their sampling methods, identification abilities, and the species and commodities they target (Whattam *et al.*, 2014; Turner *et al.*, 2021). Nonetheless, border interception records provide a unique window into the unintentional movement of insects and the commodities they are associated with.

In this study we combined interception records from six regions distributed across four continents to provide the first comprehensive overview of insect-commodity associations in international trade and travel. Most studies of insect commodity associations have considered specific groups (e.g., taxa or feeding groups) of insects arriving in a single country, often on a pre-selected suite of commodities. Bark- and wood-boring insects (e.g., Haack, 2006; Messiner *et al.*, 2008; Roques, 2010; Liebhold *et al.*, 2012; Lawson *et al.*, 2018; Meurisse *et al.*, 2019; Krishnankutty *et al.*, 2020), agricultural pests (e.g., Caton *et al.*, 2006; McCullough *et al.*, 2006; Kenis *et al.*, 2007; Smith *et al.*, 2007; Areal *et al.*, 2008; DeNitto *et al.*, 2015) and ants (e.g., Suarez *et al.*, 2001; Ward *et al.*, 2006; Suhr *et al.*, 2019; Yang *et al.*, 2019; Lee *et al.*, 2020) have been targeted in particular, likely due to the damage to forestry, agriculture and infrastructure that these taxa can cause (e.g., Jetter *et al.* 2002; Aukema *et al.*, 2011; Bradshaw *et al.*, 2016; Paini *et al.*, 2016). In addition to using a standardised system for commodity classification, the broad taxonomic and geographic coverage of interceptions in this study could potentially improve efforts to make predictions about insect introduction pathways. Our aims are to: 1) quantify the richness and diversity of insect species transported with relevant commodities, and 2) ascertain whether commodity associations vary among pathways (e.g., cargo vs. baggage vs. mail), 3) determine if key commodities vary among insect species, and groups of species, and 4) evaluate whether commodity associations are related to insect phylogeny.

Methods

Data acquisition and cleaning

We analysed records of insects detected during inspections of international air and sea cargo, mail, vessels and passenger baggage at ports of entry. The data consist of interceptions at air, land and maritime ports from 1960 to 2019 in Australia, New Zealand, member countries of the European and Mediterranean Plant Protection Organisation (EPPO), Japan, the United States of America, and Canada. As the number of individuals detected is not recorded in most regions, each interception represents a single arrival event per species. The insects discovered are destroyed, so while interceptions can be considered a proxy for species' unobserved arrival, they do not directly represent introductions. We included only interceptions between 1960 and 2019 for the years where records where available in each region (Appendix S1: Table S1), where the insect was identified to species level, with information available on the associated commodity. This timeframe corresponds to a period of increased globalization and trade openness (Baldwin and Martin, 1999; Klasing and Milionis, 2014; Feenstra *et al*., 2015). For most analyses, interceptions of genera with no members identified to species level were also included, as they represent at least one additional species.

We standardized insect taxonomic names across years and recording regions according to the Global Biodiversity Information Facility (GBIF) backbone taxonomy (GBIF Secretariat, 2019) using the taxize (Chamberlain and Szocs, 2013) and rgbif R packages (Chamberlain *et al*., 2021). GBIF has good coverage of insect taxonomy. While the taxonomic names are not always the most recent, we prioritized standardising to unique genus-species names. The process was largely automated, but occasional unmatched species were corrected manually, and a small proportion of synonyms may still be present.

We standardised commodity descriptions using the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods (World Customs Organization, 2021) and subsequently grouped commodity codes into broad classes based on the type of product (Appendix S1: Figure S1). The HS is a hierarchical system of six-digit codes, where the first two digits (HS-2) identify the chapter goods are classified in (e.g., 08: Fruit and nuts, edible; peel of citrus fruit or melons). Some level of misclassification due to manual errors may remain. Standardised classification based on HS codes provides commodity descriptions that can easily be integrated with trade data, and facilitates comparisons across countries and among studies. All analyses were conducted at the level of HS-2 codes or broad commodity classes.

Pooling data across interception regions

There are regional differences in inspection methods and targets, the sources, volume and nature of imports, and the years covered (Appendix S1: Table S1, Turner *et al*., 2021). However, the main commodity types associated with insects are similar across all regions, with the majority being plants, wood, and related products (Appendix S1: Figure S2). To test if species share similar commodity associations across regions despite the differences, we analysed the 59 species intercepted more than 20 times in two or more regions. We included a separate commodity profile for each region in which a species was intercepted. We used a partial constrained correspondence analysis (CCA) in the vegan package (Oksanen *et al*., 2019) to estimate the variance in commodity associations explained by species, once the effect of interception region is removed. A CCA relates a matrix of species' abundance or occurrence to a matrix of explanatory variables. Partial CCA is an extension of this method where you can control for the influence of conditioning variables in an additional matrix (Legendre and Legendre, 2012). Pooling the interception records across countries allows us to analyse insect arrivals based on a much wider range of taxa and commodities, and to generalize across regions. As there was an overall similarity in the commodities recorded, and species shared similar commodity associations across regions, we pooled the data for further analysis.

Estimating species richness and diversity

We used rarefaction and extrapolation methods to estimate total species richness (i.e., the number of species intercepted) and species diversity (i.e., the number and relative abundance of species) associated with different commodities, using the iNEXT package (Hsieh *et al.,* 2016). The ChaoRichness() function estimates the asymptote of rarefaction and extrapolation curves and the associated confidence intervals based on the methods proposed in Chao (1984, 1987), giving a conservative lower bound for undetected species richness. Shannon's diversity index considers both the number of species (richness) and their relative abundance (evenness), which helps to distinguish between commodities where species are transported with a similar frequency, and commodities where only a few species are commonly intercepted. The ChaoShannon() function estimates Shannon diversity based on the method proposed by Chao *et al*. (2013). In addition to the commodity type, the pathway a commodity arrives through is likely to influence which species have the opportunity to be transported. The relevant pathway was recorded for most interceptions in Australia and the USA. Only interceptions classed as cargo, passenger baggage or international mail were comparable between the two countries. We estimated the species richness and Shannon diversity associated with commodities in each of these pathways as above. To compare the differences in taxonomic composition we carried out a PERMANOVA using the adonis2() function with Bray-Curtis distances in the vegan package (Oksanen *et al*., 2019) for orders intercepted with the five commodity classes found in all three pathways (Figure 1).

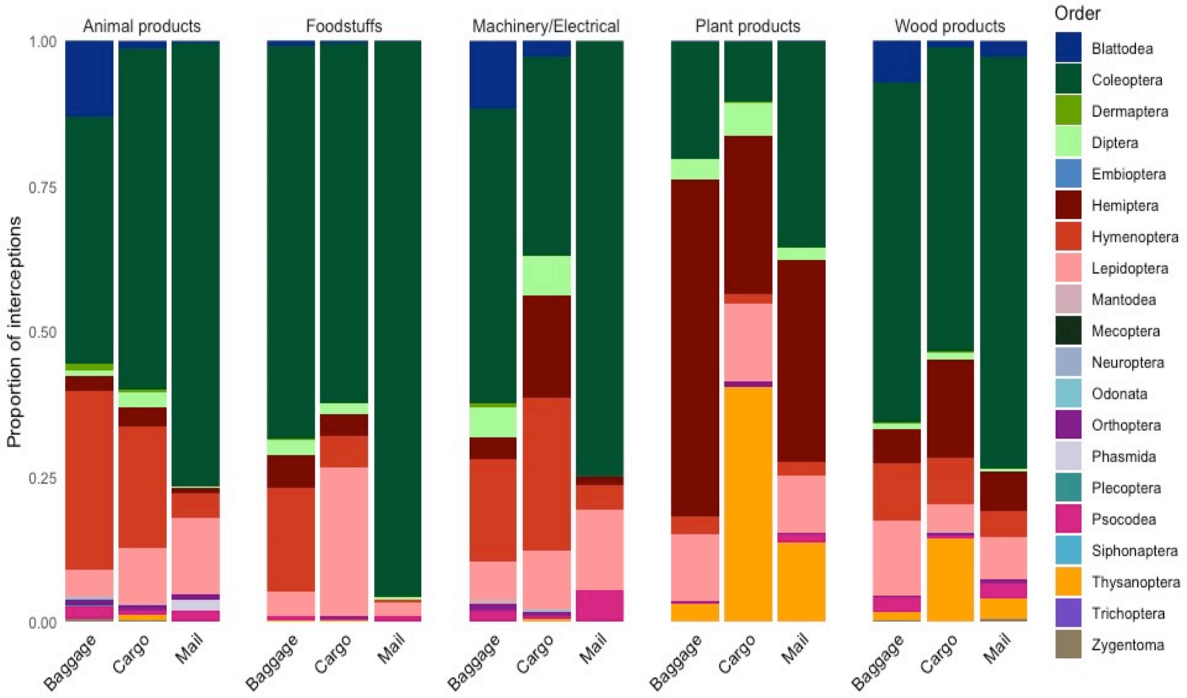

Figure 1. The taxonomic composition of interceptions on commodities arriving through the baggage, cargo and mail pathways in Australia and the USA. The bars are coloured by the proportion of interception events for each order. Only commodity classes with more than 20 interceptions in all three pathways are shown.

Phylogenetic signal of commodity associations

Phylogenetic signal can be defined as the tendency for related species to resemble each other more than they resemble species drawn at random from the tree (Bloomberg & Garland, 2002). To test whether related species share similar commodity associations, we created a tree based on the taxonomic structure of species using the as.phylo() function in the ape package (Paradis and Schliep, 2018), adding branch lengths with the compute.brlen() function. We combined the taxonomic tree with each species' coordinates from the CA, and tested for phylogenetic signal using Abouheif's Cmean in the phylosignal package (Keck *et al*., 2016). The Cmean index was compared to the null hypothesis that the trait values are randomly distributed in the taxonomy (Keck *et al*., 2016). Molecular time estimates in Timetree.org (Kumar *et al*., 2017) represent a synthesis of published divergence time estimates (Hedges *et al*., 2015). We created an additional phylogenetic tree for the 150 species with available molecular time estimates (Appendix S1: Table S2), and tested for a phylogenetic signal to commodity associations as above.

We used three separate CCAs in the vegan package (Oksanen *et al.*, 2019) to determine at what taxonomic level species share similar commodity associations, and the degree of variance explained by higher taxonomic levels. For each analysis of species "commodity profiles", species' order, family, or genus was the single constraining variable. Taxa including only a single species were excluded from these analyses. The statistical significance of each model was assessed using a permutation test for CCA in the same package.

Correspondence analysis and hierarchical clustering

To explore the relationship between species and the commodities they are transported with, we carried out a correspondence analysis (CA) using the ade4 package (Dray and Dufour, 2007). We calculated the proportion of interceptions on each HS-2 commodity group for each species, in order to compare their "commodity profiles" using the relative number of interceptions per commodity. Species with less than 20 interceptions were excluded as this provides insufficient replication to characterize commodity associations. There were 1,242 species intercepted a sufficient number of times for analysis. The first eight axes of the CA were retained. We used a hierarchical agglomerative clustering analysis in the cluster package (Maechler *et al.*, 2019) to identify species associated with similar suites of commodities. Species were clustered based on their coordinates in the CA, using the agnes() function with Ward's clustering method (Kaufman and Rousseeuw, 1990). We used the permutation test introduced by Greenacre (2011) to determine whether non-random levels of clustering were present, and if so, to indicate at which level the resulting tree can be cut to give the optimal number of clusters. All analyses were conducted in R (R Core Team, 2017) and figures produced using the ggplot2 package (Wickham, 2009).

Results

The dataset comprised 1,902,392 interception events, representing commodity associations for 7,231 species and 1,708 additional genera with no members identified to species level. The species intercepted were mainly Coleoptera (3165 species), Hemiptera (2708 species) and Lepidoptera (1103 species), but also included members of 19 other insect orders. Insects were intercepted on 80 different HS-2 commodity groups, belonging to 14 different commodity classes (Appendix S1: Table S3). With the interception region included as a conditioning variable, species explained 46.7 % of the variance in commodity associations, while the interception region explained just 12.3 % of the variance in commodity associations. Both variables explained significantly more variance than expected by chance (permutation test for CCA with 999 permutations, interception region: $F = 4.15$, $p = 0.001$, species: $F = 1.44$, $p = 0.001$).

Plant products (see Table 1 for description of commodity groups) transported by far the most species, followed by wood products, stone and glass, and machinery and electricals. Textiles were associated with much lower species richness, but transported the highest insect diversity. Animal products and foodstuffs showed similar patterns (Figure 2). Within the broad categories of plant products and wood products, the HS-2 commodities transporting the greatest species richness were live plants and cut flowers (HS 06), fruit and nuts (HS 08), vegetables (HS 07), wood and articles of wood (HS 44), and coffee, tea, herbs and spices (HS 09). Vegetable fibres (HS 53), plaiting materials (HS 46) and vegetable products and bamboo (HS 14) transported a high diversity of insects relative to species richness (Figure 3).

While plant products and wood products were associated with the highest richness and diversity across all three pathways (Appendix S1: Figure S5), there were some differences for HS-2 commodities within these categories (Appendix S1: Figure S6). Wood and articles of wood (HS 44) transported the greatest number of species through mail, whereas in passenger baggage live plants and cut flowers (HS 06), wood and articles of wood (HS 44), fruit and nuts (HS 08), vegetables (HS 07) and coffee, tea, herbs and spices (HS 09) all transported high numbers of species (Appendix S1: Figure S6). These same commodities were important in cargo, with the most species associated with live plants and cut flowers (HS 06), and fruit and nuts (HS 08). Wood and articles of wood were associated with the greatest insect diversity in all three pathways (Appendix S1: Figure S6). The exact species intercepted on the same commodity types varied between cargo, baggage and mail (Appendix S1: Figure S4). However, while the commodity class had a significant effect on the taxonomic composition of insects (PERMANOVA with 9999 permutations, $F = 2.48$, $p = 0.01$), we found no significant effect of pathway (PERMANOVA with 9999 permutations, $F = 0.58$, $p = 0.83$).

Table 1. Key commodity classes associated with insect movement, and the HS-2 commodity groups belonging to each class.

Commodity class	HS-2 code	HS-2 code and full description according to the harmonized system
Animal products	01 Live animals, 02 Meat, 03 Fish/crustaceans, 04 Dairy/eggs/honey, 05 Animal products, 41 Hides/skins, 42 Leather	01 Animals; live, 02 Meat and edible meat offal, 03 Fish and crustaceans, molluscs and other aquatic invertebrates, 04 Dairy produce; birds' eggs; natural honey; edible products of animal origin, not elsewhere specified or included, 05 Animal originated products; not elsewhere specified or included, 41 Raw hides and skins (other than furskins) and leather, 42 Articles of leather; saddlery and harness; travel goods, handbags and similar containers; articles of animal gut (other than silk-worm gut)
Plant products	06 Live plants/cut flowers, 07 Vegetables, 08 Fruit/nuts, 09 Coffee/ tea/herbs/spices, 10 Cereals, 11 Flours, 12 Seeds/ grains/medicinal plants, 13 Gum/resin, 14 Vegetable products and bamboo, (1111) soil around plants, 53 Vegetable fibres	06 Trees and other plants, live; bulbs, roots and the like; cut flowers and ornamental foliage, 07 Vegetables and certain roots and tubers; edible, 08 Fruit and nuts, edible; peel of citrus fruit or melons, 09 Coffee, tea, mate and spices, 10 Cereals, 11 Products of the milling industry; malt, starches, inulin, wheat gluten, 12 Oil seeds and oleaginous fruits; miscellaneous grains, seeds and fruit, industrial or medicinal plants; straw and fodder, 13 Lac; gums, resins and other vegetable saps and extracts, 14 Vegetable plaiting materials; vegetable products not elsewhere specified or included, (1111) soil around plants, 53 Vegetable textile fibres; paper yarn and woven fabrics of paper yarn
Foodstuffs	15 Oils/fats, 16 Meat/ fish/crustacean preparations, 17 Sugars,	15 Animal or vegetable fats and oils and their cleavage products; prepared animal fats; animal or vegetable waxes, 16 Meat, fish or crustaceans, molluscs or other aquatic invertebrates; preparations thereof,

	18 Cocoa, 19 Cereal/flour preparations, 20 Vegetable preparations, 21 Food preparations, 22 Beverages/vinegar, 23 Fodder/vegetable residue, 24 Tobacco	17 Sugars and sugar confectionery, 18 Cocoa and cocoa preparations, 19 Preparations of cereals, flour, starch or milk; pastrycooks' products, 20 Preparations of vegetables, fruit, nuts or other parts of plants, 21 Miscellaneous edible preparations, 22 Beverages, spirits and vinegar, 23 Food industries, residues and wastes thereof; prepared animal fodder, 24 Tobacco and manufactured tobacco substitutes
Wood products	44 Wood/articles of wood, 45 Cork, 46 Plaiting materials, 47 Wood pulp, 48 Paper, 49 Printed matter	44 Wood and articles of wood; wood charcoal, 45 Cork and articles of cork, 46 Manufactures of straw, esparto or other plaiting materials; basketware and wickerwork, 47 Pulp of wood or other fibrous cellulosic material; recovered (waste and scrap) paper or paperboard, 48 Paper and paperboard; articles of paper pulp, of paper or paperboard, 49 Printed books, newspapers, pictures and other products of the printing industry; manuscripts, typescripts and plans
Textiles	50 Silk, 51 Wool, 52 Cotton, 54 Synthetic fabric, 56 Twine/ felt/rope/cables, 57 Carpets, 61 Clothing, knitted, 62 Clothing, not knitted, 63 Textile articles, tents	50 Silk, 51 Wool, fine or coarse animal hair; horsehair yarn and woven fabric, 52 Cotton, 54 Man-made filaments; strip and the like of man-made textile materials, 56 Wadding, felt and nonwovens, special yarns; twine, cordage, ropes and cables and articles thereof, 57 Carpets and other textile floor coverings, 61 Apparel and clothing accessories; knitted or crocheted, 62 Apparel and clothing accessories; not knitted or crocheted, 63 Textiles, made up articles; sets; worn clothing and worn textile articles; rags
Stone/Glass	68 Stone/plaster, 69 Ceramics, 70 Glass	68 Stone, plaster, cement, asbestos, mica or similar materials; articles thereof, 69 Ceramic products, 70 Glass and glassware

Machinery/ Electrical	84 Machinery, 85 Electricals	84 Nuclear reactors, boilers, machinery and mechanical appliances; parts thereof, 85 Electrical machinery and equipment and parts thereof; sound recorders and reproducers; television image and sound recorders and reproducers, parts and accessories of such articles

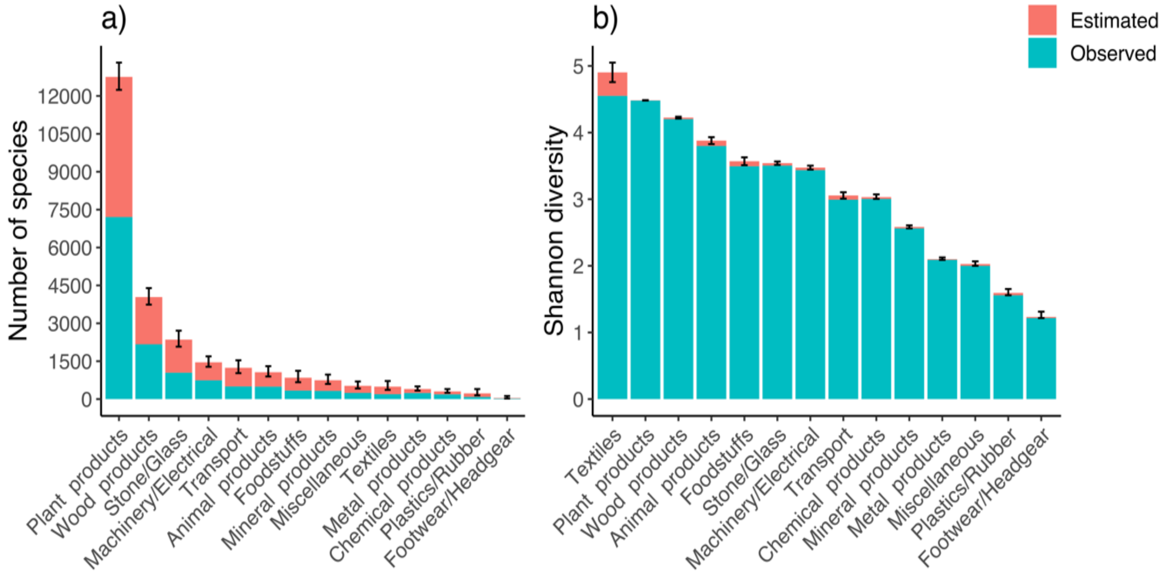

Figure 2. a) The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red) transported with each commodity class, b) the observed (blue), and estimated additional undetected Shannon diversity (red) transported with each commodity class. The error bars indicate the standard error around the estimates of total richness and diversity.

Commodity associations were non-randomly distributed among species, showing a phylogenetic signal both for the tree with relatedness based on taxonomy (Abouheif's Cmean 0.21 – 0.52, $p = 0.001$), and for the subset of species with information available on phylogenetic divergence times (Abouheif's Cmean 0.23 – 0.49, $p = 0.001$). The genus a species belongs to explained 44.3 % of the variance in species' commodity associations, while family explained 26.3 % and order explained just 6.7 % (see Appendix S1: Table S4 for regional differences). All three taxonomic levels explained significantly more variance than expected by chance (permutation test for CCA with 999 permutations, genus: $F = 2.47$, $p = 0.001$, family: $F = 3.61$, $p = 0.001$, order: $F = 9.64$, $p = 0.001$).

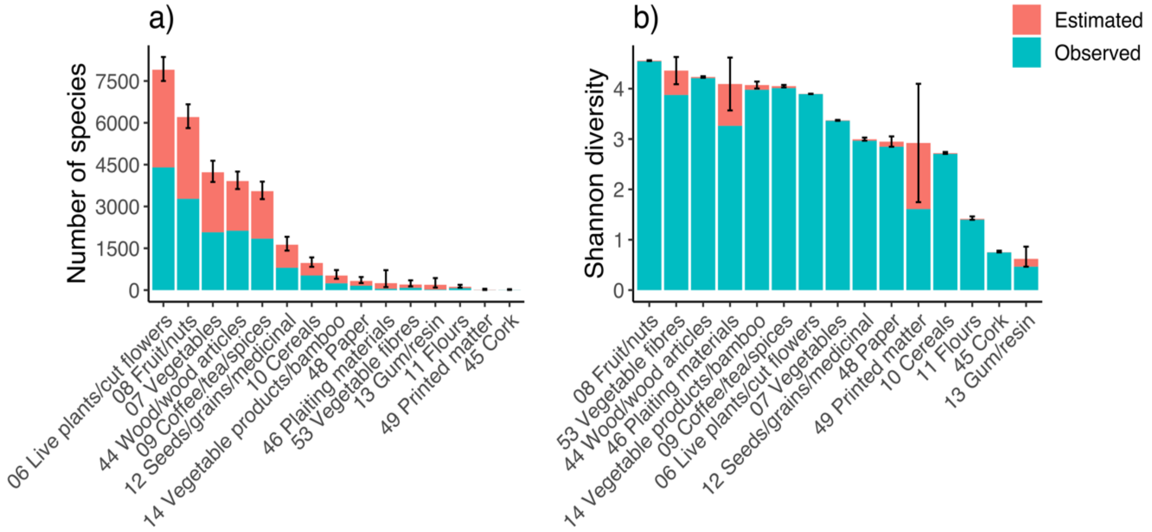

Figure 3. a) The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red), and b) the observed, and estimated additional undetected Shannon diversity transported with each HS-2 commodity group classed as plant products or wood products. The error bars indicate the standard error around the estimates of total richness and diversity.

We found 11 distinct clusters of species transported with similar suites of commodities (Figure 4). The first cluster consisted of 465 species most frequently intercepted with live plants and cut flowers (HS 06), but which were also frequently associated with fruit and nuts (HS 07). These species belong to the orders Hemiptera, Coleoptera, Lepidoptera, Thysanoptera, Hymenoptera, Diptera, Orthoptera, and Dermaptera, in decreasing order of species richness. The second cluster contained 64 species of Coleoptera, Lepidoptera, Hemiptera, Thysanoptera, Diptera, and Hymenoptera, which were most frequently intercepted with vegetables (HS 07). The third cluster was most often transported with ceramics (HS 69) and wood and articles of wood (HS 44), and consisted of 51 species of Coleoptera, Hymenoptera, Hemiptera, Lepidoptera, Blattodea, Orthoptera and Diptera. The fourth cluster of 53 species of Hemiptera, Coleoptera, Orthoptera and Lepidoptera were most frequently transported with ceramics (HS 69). The fifth cluster contained 107 species of Coleoptera, Hemiptera, Hymenoptera, and Lepidoptera which were mainly associated with wood and articles of wood (HS 44). The sixth cluster consisted of 23 species of Hymenoptera, Lepidoptera, Diptera, Coleoptera, Blattodea, Orthoptera and Hemiptera, which were most frequently transported with machinery (HS 84). The seventh cluster consisted of 89 species most frequently transported with coffee, tea, herbs and spices (HS 09), belonging to the orders Hemiptera, Thysanoptera, Lepidoptera, Coleoptera and Diptera. The eighth cluster consisted of 180 species of Hemiptera, Coleoptera, Thysanoptera, Lepidoptera, Diptera, Hymenoptera and Dermaptera, which were most often associated with fruit and nuts (HS 08). The ninth cluster of 162 species were most frequently associated with live plants and cut flowers (HS 06), and belonged to Hemiptera, Coleoptera, Lepidoptera, Diptera, Orthoptera, Thysanoptera, Hymenoptera and Blattodea. The tenth cluster consisted of 39 species of Coleoptera, Psocodea, Blattodea, Zygentoma, Hymenoptera, Lepidoptera and Hemiptera, and were most often intercepted with vegetable products and bamboo (HS 14). The eleventh cluster consisted of just nine species of Coleoptera and Diptera, most frequently associated with meat and crustacean preparations (HS 16). Please refer to Appendix S1: Figure S3 for more detail.

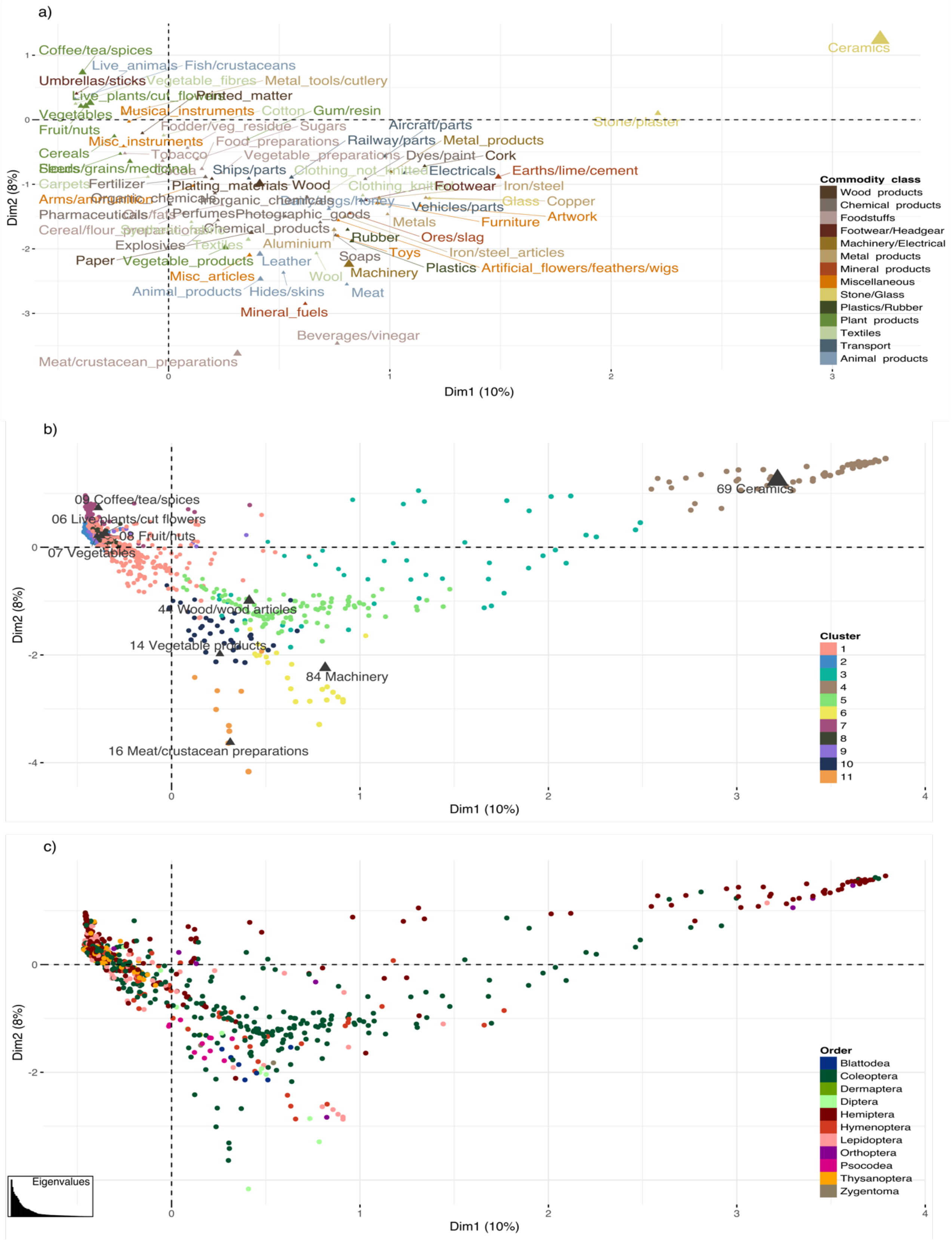

Figure 4. A correspondence analysis of species' commodity associations, where a) the HS-2

commodity groups are coloured by the broad commodity class they belong to and the size of the triangles relate to their total contribution to the principal components, b) species are shown as circles coloured by the cluster they belong to, and the HS-2 commodity groups species in each cluster are intercepted on most frequently are labelled, and c) species are shown as circles coloured by the order they belong to.

Discussion

The establishment of intentionally introduced organisms can be managed through regulations limiting importation and possession. However, prevention of unintentionally introduced organisms is more complex. It is first necessary to identify the major pathways by which these organisms are introduced, which individual national biosecurity agencies typically accomplish via pathway risk analyses (Essl *et al.*, 2020; Hulme, 2009). We pooled border interception records spanning four continents to improve our knowledge of the commodities responsible for unintentional insect introductions. We found that plant and wood products were the dominant means of movement through international trade and travel. While this is well-known for specific insect groups (e.g. Kiritani & Yamamura, 2003; Roques, 2010; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019), our results highlight the wide range of taxa transported with these commodity types. Plant products and wood products were associated with the highest species richness in cargo, in international mail and in passenger baggage, supporting their status as important targets for management across pathways. However, these were not the main commodities transporting all insect species, and many species were primarily associated with distinct commodity groups within these broad categories. This suggests that detailed information about relevant commodities is required for preventing the introduction of specific insect taxa.

The movement of plants and wood have long been recognized as important pathways for insect invasions (Kiritani & Yamamura, 2003; Roques, 2010; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019). National biosecurity programs direct considerable effort towards limiting the accidental movement of insects through quarantine, inspection, mandatory phytosanitary treatments and other extensive pre-border measures (Sequeira and Griffin, 2014), harmonized by the International Plant Protection Convention and other bodies (Hulme 2011). We found that live plants and cut flowers, fruit and nuts, wood and articles of wood, vegetables, and coffee, tea, herbs and spices, in particular transport a high number of species. While there is considerable variation in the insect taxa and commodity types considered in the literature, the importance of live plants (Liebhold *et al*., 2012; Eschen *et al.* 2015; Meurisse *et al*., 2019), cut flowers (Work *et al*., 2005; McCullough *et al*., 2006; Roques and Auger-Rozenberg, 2006; Kenis *et al*., 2007; Areal *et al*., 2008; Hong *et al*., 2012; Lee *et al*., 2016; Suhr *et al*., 2019), wood packaging material (Brockerhoff *et al*., 2006; Haack, 2006; Messiner *et al*., 2008; Lawson *et al*., 2018; Krishnankutty *et al*., 2020), fruits and vegetables (Work *et al*., 2005; McCullough *et al*., 2006; Roques and Auger-Rozenberg, 2006; Kenis *et al*., 2007; Lee *et al*., 2016; Suhr *et al*., 2019) and seeds (McCullough *et al*., 2006; Kenis *et al*., 2007; Franić *et al*., 2019) have been recognised previously. With the addition of coffee, tea, herbs and spices as key plant products, our results support that these commodities are major sources of insect introductions worldwide.

While the same commodity types were generally important across pathways, the species richness and diversity associated with specific HS-2 commodity groups varied (Appendix S1: Figure S6). The taxonomic composition of species associated with a commodity also differed between pathways, for example proportionally more Hemiptera were associated with wood products in cargo than in baggage or mail. Commodities are often subject to different production and pest management practices depending on the pathway. Pathways also necessarily differ in the exact type, volume, treatment, and transport time of commodities, which in turn filters which species are present. For example, fresh fruits imported as commercial cargo typically undergo stringent care during production, and sometimes mandatory phytosanitary treatments to reduce pest risk. Fresh fruits arriving in baggage, on the other hand, may not have been commercially produced, and are controlled through inspection alongside public messaging. Pathway-specific variation in pest management practices during the production, transport and arrival of commodities are likely to strongly influence which species are encountered during inspections.

The movement of textiles (Caton *et al*., 2006), and abiotic commodities like machinery and building materials (McCullough *et al*., 2006), containers and used vehicles (Brockerhoff *et al*., 2006; Ward *et al*., 2006), and tiles (Work *et al*., 2005; Haack, 2006) have also been identified as important pathways for insect introductions. Ordination largely separated biotic commodities like plant products and foodstuffs from wood products, and various abiotic commodities based on the associated species (Figure 4). The similarity in species associated with wood products and abiotic commodities may be due to the presence of wood packaging materials during transport. Up to 70 % of all goods traded internationally (USDA cited in Eyre *et al*., 2018) are accompanied with some form of wood packaging, which offers a suitable substrate for many insect contaminants and hitchhikers. We are unable to distinguish between species transported with the packaging or the commodity itself based on the interception records, so the associated risk could also stem from the packaging. However, infestation rates of wood packaging materials are low (e.g., 0.17 to 0.25% in the United States prior to ISPM15 (Haack *et al*. 2014)) and are unlikely to be a significant proportion of the records we assess here. We also found that textiles transport a particularly high diversity of insects relative to species richness, along with animal products and foodstuffs. It's likely that many species are only rarely associated with a given commodity, and due to the lower propagule pressure will be less likely to establish (Kolar and Lodge, 2001; Lockwood *et al.,* 2005). Commodities such as textiles where species are more evenly transported may be sources of increased introduction risk.

However, a greater number of species introductions does not necessarily translate into greater impacts. *National Plant Protection Organizations rely on species-specific risk assessments to predict* the potential damage caused by insects known to be associated with particular commodities. It should also be noted that during the period from which we sourced data (1960-2019), there has been considerable progress in implementation of new biosecurity practices that have likely reduced rates of commodity contamination and total numbers of species entering. For example, the harmonized international standard ISPM-15 established by the International Plan Protection Convention specifies phytosanitary treatments for wood packaging, and has resulted in a substantial decrease in levels of wood-boring insects present in this material (Haack et al. 2014). As another example, during this period the US Department of Agriculture has phased in new quarantine procedures for live plant imports that prohibit importation of plants in a large number of genera until risk analyses can be performed (USDA, 2021). Thus, numbers of species associated with commodities likely changed during the period from which our data was sourced.

Prevention strategies that focus on high-risk pathways alongside quarantine protocols targeting individual taxa are crucial for limiting arrivals of new and damaging species (e.g. Keller *et al*., 2009). Aichi Biodiversity Target 9 aimed that “by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment” (Convention on Biological Diversity, 2010). This clearly remains a work in progress (e.g., Tittensor *et al.*, 2014), and continued research into pathway identification and management is necessary. Economic analyses are needed to evaluate whether the costs of additional biosecurity controls are smaller than the benefits of preventing invasions (Welsh *et al.*, 2021). Moreover, future work could improve our estimates of species richness and diversity associated with different commodities by adjusting for import volume. The species contaminating or hitchhiking with a commodity are necessarily a subset of the species present in the region it originated from, or potentially from intermediate stops along the way. Comparing the size and composition of species pools arriving from different world regions alongside associated trade volumes would help further explain patterns of introduction risk. We also observed that the degree of diversity in commodity associations varied considerably between taxa. Quantifying this variation would help to adjust the level of detail required for risk assessments and predictive modelling of different insect groups.

Species intercepted during port-of-entry inspections represent only a small proportion of the pool of insects arriving in a region (Kenis *et al.*, 2007), and many species which arrive infrequently are likely never detected (Brockerhoff *et al.*, 2014). The exact pathways of many new introductions are therefore unknown, and we may not have extensive knowledge about the commodities they are transported with. On condition that related insects tend to be transported with similar suites of commodities, species with known commodity associations could provide clues to the dispersal pathways of their more poorly observed relatives. Our results show that related species do to some extent share similar commodity associations, although there remains a lot of variation within insect taxa and interception regions. The similarities in commodity associations within genera could supply valuable information for targeting pathway management of new species.

Interceptions provide direct evidence of an association between an organism and a commodity, but come with a number of limitations. Inspections often focus on commodities and pathways that *a priori* are considered high-risk, and may preferentially, or exclusively, record interceptions according to lists of regulated goods or regulated pest species (Eschen *et al*., 2015). As the movement of plant and wood products are recognised as major pathways of insect introductions, they may be more frequently targeted for inspection. The greater intensity of inspections may thus lead to more interceptions irrespective of actual risk, creating a feedback to targeting of these commodities. It is difficult to correct for inspection effort as practices vary between countries and pathways, and are adapted over time as risk assessments are updated, or new biosecurity policies come into force. Additionally, our analyses focus on records identified to species level, and might not be representative of less easily identifiable taxa. While our results are based on insects arriving in six different regions, these are high-income countries and may not be representative of introductions to many developing nations. Unfortunately, negative inspections were not recorded. Randomized, statistically sound inspection systems such as the USDA Agricultural Quarantine Inspection Monitoring system (USDA, 2011) would provide greater power to quantify pathway risks when comparing and combining interception records, but are only focused on a few pathways in a few countries (Griffin, 2020).

The breadth and focus of inspections varies between regions, and alongside differences in import volume, production practices, trade partners, and biosecurity measures, are likely to influence the subset of commodity associations we observe (Saccaggi *et al*., 2016; Turner *et al*., 2021). In Europe, economically harmful plant-pests are “black-listed” from entering and being moved around the continent, and interceptions are largely restricted to these quarantine species (European Commission, 2002). Inspectors must check all consignments that could contain quarantine insects, but the exact sampling volumes and methods vary between the European member states (Bacon *et al*., 2012). Biosecurity programs in Australia and New Zealand operate based on “white-lists” of species that have been assessed and are considered safe (Eschen *et al*., 2015). However, from New Zealand we only had access to interceptions of ants (Formicidae) and forest insects, with a corresponding bias in associated commodities. In the USA, Canada and Japan, the system is similar to Europe in that they have “black lists” of quarantine pests (Animal and Plant Health Inspection Service, 2020; Canadian Food Inspection Agency, 2021; Ministry of Agriculture and Fisheries, 2021), but these are generally less restrictive. Records from the USA made up the majority of both interception events and individual species intercepted, and our results were strongly influenced by the commodity associations of insects arriving in the USA

(Appendix S1: Figure S7). See Appendix S1: Figures S8-S11 for more detail about regional differences.

Nevertheless, the trends in commodity associations we observed are likely to be widely applicable. We used rarefaction and extrapolation methods to estimate species richness and diversity for standardized sample sizes (Chiarucci *et al.*, 2008), so we expect the ranking of commodities to be robust. While the list of commodities and species transported is almost certainly incomplete (Eschen *et al.*, 2015), the clusters of species associated with distinct commodities are likely to be robust. In most cases, inspection is not an effective method for excluding pest arrival and establishment directly, but provides crucial information for risk assesment. Pooling interception records across regions captures complementary aspects of the human-mediated dispersal of insects, rather than focussing on insects arriving in a single region. The broad range of species and commodities intercepted provide a meaningful overview of the variation in commodity associations between and within taxa, as well as between pathways.

Conclusions

Pathway analysis and management are powerful strategies for predicting and preventing new introductions of contaminant and hitchhiking insects. While knowledge of the exact pathways of unintentional introductions is scarce, pooling interception records across multiple regions provides a unique source of information on relevant commodities. Plant and wood products are important commodities across the cargo, baggage and mail pathways. Live plants and cut flowers, fruit and nuts, wood and articles of wood, vegetables, and coffee, tea, herbs and spices in particular transport a high number of species. Commodities associated with high insect diversity, such as textiles, may be additional priorities for control measures.

While plants, wood and their associated products are important overall, the key targets for pathway management will not be the same for all alien species. Similarities in commodity associations within insect genera may provide valuable information for the management of potential previously unknown invaders. Our results highlight the wide range of commodities that are potential sources of new insect introductions, and the need for detailed information on relevant dispersal commodities to effectively limit future insect introductions.

Acknowledgements

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Supplementary material: chapter 1

Table S1. A description of the interception records available for each of the six regions.

Interception region	Data collection	Years covered	Total interception events	Orders	Species (+ additional genera)	% of species with > 20 interceptions	Commodity classes	HS-2 commodity groups	Source countries	Pathway information available
Australia	Department of Agriculture, Water and Environment	2003-2016	56955	19	1740	12.0 %	13	37	-	Yes
Canada	Canadian Food Inspection Agency	1997-2019	3165	12	926	2.4 %	9	29	89	No
European Plant Protection Organization (EPPO)	Various EPPO member countries	1995-2010	9464	7	303	10.2 %	2	5	116	No
Japan	Ministry of Agriculture, Forestry and Fisheries	1997-2017	289430	9	1235	18.9 %	6	14	128	No
New Zealand	Scion BUGS database, New Zealand Ministry for Primary Industries (or predecessors recorded under different names)	1960-2013 Formicidae 1960-2000 Forest insects	11759	3	553	12.7 %	14	62	122	No
United States of America	US Department of Agriculture, Animal & Plant Health Inspection Service, Department of Homeland Security, Customs and Border Protection	1998-2018 1960-2019 Formicidae 1960-1982 Thysanoptera 1960-2000 Forest insects	1531619	15	6827	12.9 %	14	78	220	Yes

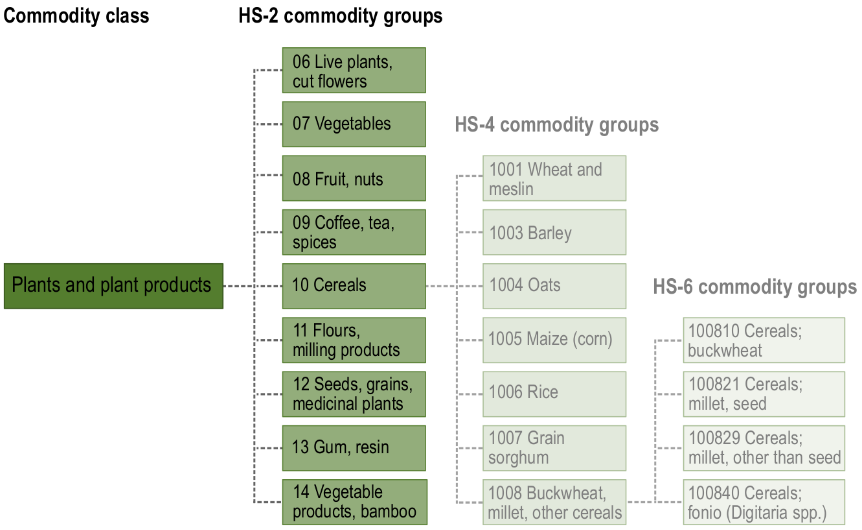


Figure S1. Plants and plant products as an example of the hierarchical classification of commodities. The first level of classification is based on the broad class of products, which is then further divided according to the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods.

Table S2. The 150 species for which estimates of molecular divergence time were available from Timetree.org.

Species	Genus	Family	Order
Blatta orientalis	*Blatta*	Blattidae	Blattodea
Neostylopyga rhombifolia	*Neostylopyga*	Blattidae	Blattodea
Periplaneta americana	*Periplaneta*	Blattidae	Blattodea
Periplaneta australasiae	*Periplaneta*	Blattidae	Blattodea
Blattella germanica	*Blattella*	Ectobiidae	Blattodea
Supella longipalpa	*Supella*	Ectobiidae	Blattodea
Cryptotermes brevis	*Cryptotermes*	Kalotermitidae	Blattodea
Coptotermes formosanus	*Coptotermes*	Rhinotermitidae	Blattodea
Porotermes quadricollis	*Porotermes*	Stolotermitidae	Blattodea
Lyctus brunneus	*Lyctus*	Bostrichidae	Coleoptera
Cylas formicarius	*Cylas*	Brentidae	Coleoptera
Hylotrupes bajulus	*Hylotrupes*	Cerambycidae	Coleoptera
Acanthoscelides argillaceus	*Acanthoscelides*	Chrysomelidae	Coleoptera
Acanthoscelides obtectus	*Acanthoscelides*	Chrysomelidae	Coleoptera
Acanthoscelides obvelatus	*Acanthoscelides*	Chrysomelidae	Coleoptera
Bruchus pisorum	*Bruchus*	Chrysomelidae	Coleoptera
Callosobruchus chinensis	*Callosobruchus*	Chrysomelidae	Coleoptera
Callosobruchus maculatus	*Callosobruchus*	Chrysomelidae	Coleoptera
Callosobruchus phaseoli	*Callosobruchus*	Chrysomelidae	Coleoptera
Megabruchidius tonkineus	*Megabruchidius*	Chrysomelidae	Coleoptera
Stator limbatus	*Stator*	Chrysomelidae	Coleoptera
Necrobia rufipes	*Necrobia*	Cleridae	Coleoptera
Harmonia axyridis	*Harmonia*	Coccinellidae	Coleoptera
Dendroctonus pseudotsugae	*Dendroctonus*	Curculionidae	Coleoptera
Dinoplatypus pseudocupulatus	*Dinoplatypus*	Curculionidae	Coleoptera
Dryocoetes autographus	*Dryocoetes*	Curculionidae	Coleoptera
Hylurgops rugipennis	*Hylurgops*	Curculionidae	Coleoptera
Hylurgus ligniperda	*Hylurgus*	Curculionidae	Coleoptera
Hypera postica	*Hypera*	Curculionidae	Coleoptera

Platypus jansoni	*Platypus*	Curculionidae	Coleoptera
Tomicus piniperda	*Tomicus*	Curculionidae	Coleoptera
Xyleborus affinis	*Xyleborus*	Curculionidae	Coleoptera
Anthrenus verbasci	*Anthrenus*	Dermestidae	Coleoptera
Trogoderma granarium	*Trogoderma*	Dermestidae	Coleoptera
Trogoderma variabile	*Trogoderma*	Dermestidae	Coleoptera
Metamasius hemipterus	*Metamasius*	Dryophthoridae	Coleoptera
Sitophilus granarius	*Sitophilus*	Dryophthoridae	Coleoptera
Cryptolestes ferrugineus	*Cryptolestes*	Laemophloeidae	Coleoptera
Tenebrio molitor	*Tenebrio*	Tenebrionidae	Coleoptera
Tribolium castaneum	*Tribolium*	Tenebrionidae	Coleoptera
Tribolium confusum	*Tribolium*	Tenebrionidae	Coleoptera
Forficula auricularia	*Forficula*	Forficulidae	Dermaptera
Liriomyza bryoniae	*Liriomyza*	Agromyzidae	Diptera
Liriomyza huidobrensis	*Liriomyza*	Agromyzidae	Diptera
Liriomyza sativae	*Liriomyza*	Agromyzidae	Diptera
Liriomyza trifolii	*Liriomyza*	Agromyzidae	Diptera
Delia radicum	*Delia*	Anthomyiidae	Diptera
Chrysomya megacephala	*Chrysomya*	Calliphoridae	Diptera
Lucilia sericata	*Lucilia*	Calliphoridae	Diptera
Aedes aegypti	*Aedes*	Culicidae	Diptera
Aedes albopictus	*Aedes*	Culicidae	Diptera
Culex quinquefasciatus	*Culex*	Culicidae	Diptera
Drosophila melanogaster	*Drosophila*	Drosophilidae	Diptera
Atherigona orientalis	*Atherigona*	Muscidae	Diptera
Musca domestica	*Musca*	Muscidae	Diptera
Hermetia illucens	*Hermetia*	Stratiomyidae	Diptera
Anastrepha obliqua	*Anastrepha*	Tephritidae	Diptera
Bactrocera correcta	*Bactrocera*	Tephritidae	Diptera
Bactrocera cucurbitae	*Bactrocera*	Tephritidae	Diptera
Bactrocera dorsalis	*Bactrocera*	Tephritidae	Diptera
Bactrocera oleae	*Bactrocera*	Tephritidae	Diptera
Bactrocera zonata	*Bactrocera*	Tephritidae	Diptera
Ceratitis capitata	*Ceratitis*	Tephritidae	Dipt*era*
Dacus ciliatus	*Dacus*	Tephritidae	Diptera
Aleurodicus dispersus	*Aleurodicus*	Aleyrodidae	Hemiptera
Bemisia tabaci	*Bemisia*	Aleyrodidae	Hemiptera
Trialeurodes vaporariorum	*Trialeurodes*	Aleyrodidae	Hemiptera
Acyrthosiphon pisum	*Acyrthosiphon*	Aphididae	Hemiptera
Aphis aurantii	*Aphis*	Aphididae	Hemiptera
Aphis craccivora	*Aphis*	Aphididae	Hemiptera
Aphis fabae	*Aphis*	Aphididae	Hemiptera
Aphis gossypii	*Aphis*	Aphididae	Hemiptera
Aphis intybi	*Aphis*	Aphididae	Hemiptera
Aphis spiraecola	*Aphis*	Aphididae	Hemiptera
Brevicoryne brassicae	*Brevicoryne*	Aphididae	Hemiptera
Eriosoma lanigerum	*Eriosoma*	Aphididae	Hemiptera
Lipaphis pseudobrassicae	*Lipaphis*	Aphididae	Hemiptera
Myzus persicae	*Myzus*	Aphididae	Hemiptera
Rhopalosiphum maidis	*Rhopalosiphum*	Aphididae	Hemiptera
Rhopalosiphum nymphaeae	*Rhopalosiphum*	Aphididae	Hemiptera
Rhopalosiphum padi	*Rhopalosiphum*	Aphididae	Hemiptera
Tinocallis takachihoensis	*Tinocallis*	Aphididae	Hemiptera
Ceroplastes japonicus	*Ceroplastes*	Coccidae	Hemiptera
Coccus hesperidum	*Coccus*	Coccidae	Hemiptera
Aonidiella aurantii	*Aonidiella*	Diaspididae	Hemiptera
Parlatoria oleae	*Parlatoria*	Diaspididae	Hemiptera
Crypticerya genistae	*Crypticerya*	Margarodidae	Hemiptera
Icerya purchasi	*Icerya*	Margarodidae	Hemiptera
Icerya seychellarum	*Icerya*	Margarodidae	Hemiptera
Lygus rugulipennis	*Lygus*	Miridae	Hemiptera
Nesidiocoris tenuis	*Nesidiocoris*	Miridae	Hemiptera
Taylorilygus apicalis	*Taylorilygus*	Miridae	Hemiptera
Insignorthezia insignis	*Insignorthezia*	Ortheziidae	Hemiptera
Megacopta cribraria	*Megacopta*	Plataspidae	Hemiptera
Dysmicoccus brevipes	*Dysmicoccus*	Pseudococcidae	Hemiptera
Ferrisia virgata	*Ferrisia*	Pseudococcidae	Hemiptera
Planococcus citri	*Planococcus*	Pseudococcidae	Hemiptera
Pseudococcus longispinus	*Pseudococcus*	Pseudococcidae	Hemiptera
Pseudococcus maritimus	*Pseudococcus*	Pseudococcidae	Hemiptera

Pyrrhocoris apterus	*Pyrrhocoris*	Pyrrhocoridae	Hemiptera
Apis cerana	*Apis*	Apidae	Hymenoptera
Apis dorsata	*Apis*	Apidae	Hymenoptera
Apis mellifera	*Apis*	Apidae	Hymenoptera
Anoplolepis gracilipes	*Anoplolepis*	Formicidae	Hymenoptera
Camponotus pennsylvanicus	*Camponotus*	Formicidae	Hymenoptera
Cardiocondyla emeryi	*Cardiocondyla*	Formicidae	Hymenoptera
Crematogaster scutellaris	*Crematogaster*	Formicidae	Hymenoptera
Linepithema humile	*Linepithema*	Formicidae	Hymenoptera
Monomorium pharaonis	*Monomorium*	Formicidae	Hymenoptera
Ochetellus glaber	*Ochetellus*	Formicidae	Hymenoptera
Oecophylla smaragdina	*Oecophylla*	Formicidae	Hymenoptera
Paratrechina longicornis	*Paratrechina*	Formicidae	Hymenoptera
Solenopsis invicta	*Solenopsis*	Formicidae	Hymenoptera
Solenopsis molesta	*Solenopsis*	Formicidae	Hymenoptera
Solenopsis xyloni	*Solenopsis*	Formicidae	Hymenoptera
Tapinoma melanocephalum	*Tapinoma*	Formicidae	Hymenoptera
Tapinoma sessile	*Tapinoma*	Formicidae	Hymenoptera
Technomyrmex albipes	*Technomyrmex*	Formicidae	Hymenoptera
Tetramorium caespitum	*Tetramorium*	Formicidae	Hymenoptera
Wasmannia auropunctata	*Wasmannia*	Formicidae	Hymenoptera
Sirex noctilio	*Sirex*	Siricidae	Hymenoptera
Urocerus gigas	*Urocerus*	Siricidae	Hymenoptera
Xeris spectrum	*Xeris*	Siricidae	Hymenoptera
Estigmene acrea	*Estigmene*	Arctiidae	Lepidoptera
Lymantria dispar	*Lymantria*	Erebidae	Lepidoptera
Phthorimaea operculella	*Phthorimaea*	Gelechiidae	Lepidoptera
Lampides boeticus	*Lampides*	Lycaenidae	Lepidoptera
Agrotis ipsilon	*Agrotis*	Noctuidae	Lepidoptera
Mythimna unipuncta	*Mythimna*	Noctuidae	Lepidoptera
Spodoptera albula	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera cosmioides	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera dolichos	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera eridania	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera exigua	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera frugiperda	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera latifascia	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera littoralis	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera litura	*Spodoptera*	Noctuidae	Lepidoptera
Spodoptera ornithogalli	*Spodoptera*	Noctuidae	Lepidoptera
Trichoplusia ni	*Trichoplusia*	Noctuidae	Lepidoptera
Pieris rapae	*Pieris*	Pieridae	Lepidoptera
Hippotion celerio	*Hippotion*	Sphingidae	Lepidoptera
Macroglossum stellatarum	*Macroglossum*	Sphingidae	Lepidoptera
Cydia pomonella	*Cydia*	Tortricidae	Lepidoptera
Calliptamus italicus	*Calliptamus*	Acrididae	Orthoptera
Acheta domesticus	*Acheta*	Gryllidae	Orthoptera
Trogium pulsatorium	*Trogium*	Trogiidae	Psocodea
Frankliniella cephalica	*Frankliniella*	Thripidae	Thysanoptera
Thrips palmi	*Thrips*	Thripidae	Thysanoptera
Ctenolepisma longicaudata	*Ctenolepisma*	Lepismatidae	Zygentoma

Table S3. The commodity classes insects were intercepted on, the HS-2 commodity codes included in each class, and their descriptions according to the Harmonized System.

Commodity class	**HS-2 code**	**HS-2 code and full description**
Animal products	01 Live animals, 02 Meat, 03 Fish/crustaceans, 04 Dairy/eggs/honey, 05 Animal products, 41 Hides/skins, 42 Leather	01 Animals; live, 02 Meat and edible meat offal, 03 Fish and crustaceans, molluscs and other aquatic invertebrates, 04 Dairy produce; birds' eggs; natural honey; edible products of animal origin, not elsewhere specified or included, 05 Animal originated products; not elsewhere specified or included, 41 Raw hides and skins (other than furskins) and leather, 42 Articles of leather; saddlery and harness; travel goods, handbags and similar containers; articles of animal gut (other than silk-worm gut)

Plant products	06 Live plants/cut flowers, 07 Vegetables, 08 Fruit/nuts, 09 Coffee/tea/herbs/spices, 10 Cereals, 11 Flours, 12 Seeds/grains/medicinal plants, 13 Gum/resin, 14 Vegetable products and bamboo, (1111) soil around plants, 53 Vegetable fibres	06 Trees and other plants, live; bulbs, roots and the like; cut flowers and ornamental foliage, 07 Vegetables and certain roots and tubers; edible, 08 Fruit and nuts, edible; peel of citrus fruit or melons, 09 Coffee, tea, mate and spices, 10 Cereals, 11 Products of the milling industry; malt, starches, inulin, wheat gluten, 12 Oil seeds and oleaginous fruits; miscellaneous grains, seeds and fruit, industrial or medicinal plants; straw and fodder, 13 Lac; gums, resins and other vegetable saps and extracts, 14 Vegetable plaiting materials; vegetable products not elsewhere specified or included, (1111) soil around plants, 53 Vegetable textile fibres; paper yarn and woven fabrics of paper yarn
Foodstuffs	15 Oils/fats, 16 Meat/fish/crustacean preparations, 17 Sugars, 18 Cocoa, 19 Cereal/flour preparations, 20 Vegetable preparations, 21 Food preparations, 22 Beverages/vinegar, 23 Fodder/vegetable residue, 24 Tobacco	15 Animal or vegetable fats and oils and their cleavage products; prepared animal fats; animal or vegetable waxes, 16 Meat, fish or crustaceans, molluscs or other aquatic invertebrates; preparations thereof, 17 Sugars and sugar confectionery, 18 Cocoa and cocoa preparations, 19 Preparations of cereals, flour, starch or milk; pastrycooks' products, 20 Preparations of vegetables, fruit, nuts or other parts of plants, 21 Miscellaneous edible preparations, 22 Beverages, spirits and vinegar, 23 Food industries, residues and wastes thereof; prepared animal fodder, 24 Tobacco and manufactured tobacco substitutes
Mineral products	25 Earths/lime/cement, 26 Ores/slag, 27 Mineral fuels	25 Salt; 57 Sulphur; earths, stone; plastering materials, lime and cement, 26 Ores, slag and ash, 27 Mineral fuels, mineral oils and products of their distillation; bituminous substances; mineral waxes
Chemical products	28 Inorganic chemicals, 29 Organic chemicals, 30 Pharmaceuticals, 31 Fertilizer, 32 Dyes/paint, 33 Perfumes, 34 Soaps, 36 Explosives	28 Inorganic chemicals; organic and inorganic compounds of precious metals; of rare earth metals, of radio-active elements and of isotopes, 29 Organic chemicals, 30 Pharmaceutical products, 31 Fertilizers, 32 Tanning or dyeing extracts; tannins and their derivatives; dyes, pigments and other colouring matter; paints, varnishes; putty, other mastics; inks, 33 Essential oils and resinoids; perfumery, cosmetic or toilet preparations, 34 Soap, organic surface-active agents; washing, lubricating, polishing or scouring preparations; artificial or prepared waxes, candles and similar articles, modelling pastes, dental waxes and dental preparations with a basis of plaster, 36 Explosives; pyrotechnic products; matches; pyrophoric alloys; certain combustible preparations
Plastics/Rubber	39 Plastics, 40 Rubber	39 Plastics and articles thereof, 40 Rubber and articles thereof
Wood products	44 Wood/articles of wood, 45 Cork, 46 Plaiting materials, 47 Wood pulp, 48 Paper, 49 Printed matter	44 Wood and articles of wood; wood charcoal, 45 Cork and articles of cork, 46 Manufactures of straw, esparto or other plaiting materials; basketware and wickerwork, 47 Pulp of wood or other fibrous cellulosic material; recovered (waste and scrap) paper or paperboard, 48 Paper and paperboard; articles of paper pulp, of paper or paperboard, 49 Printed books, newspapers, pictures and other products of the printing industry; manuscripts, typescripts and plans
Textiles	50 Silk, 51 Wool, 52 Cotton, 54 Synthetic fabric, 56 Twine/felt/rope/cables, 57 Carpets, 61 Clothing, knitted, 62 Clothing, not knitted, 63 Textile articles, tents	50 Silk, 51 Wool, fine or coarse animal hair; horsehair yarn and woven fabric, 52 Cotton, 54 Man-made filaments; strip and the like of man-made textile materials, 56 Wadding, felt and nonwovens, special yarns; twine, cordage, ropes and cables and articles thereof, 57 Carpets and other textile floor coverings, 61 Apparel and clothing accessories; knitted or crocheted, 62 Apparel and clothing accessories; not knitted or crocheted, 63 Textiles, made up articles; sets; worn clothing and worn textile articles; rags
Footwear/Headgear	64 Footwear, 66 Umbrellas/sticks	64 Footwear; gaiters and the like; parts of such articles, 66 Umbrellas, sun umbrellas, walking-sticks, seat sticks, whips, riding crops; and parts thereof
Stone/Glass	68 Stone/plaster, 69 Ceramics, 70 Glass	68 Stone, plaster, cement, asbestos, mica or similar materials; articles thereof, 69 Ceramic products, 70 Glass and glassware
Metal products	72 Iron/steel, 73 Iron/steel articles, 74 Copper, 75 Nickel, 76 Aluminium, 80 Tin, 81 Metals, 82 Metal tools/cutlery, 83 Metal products	72 Iron and steel, 73 Iron or steel articles, 74 Copper and articles thereof, 75 Nickel and articles thereof, 76 Aluminium and articles thereof, 80 Tin; articles thereof, 81 Metals; n.e.c., cermets and articles thereof, 82 Tools, implements, cutlery, spoons and forks, of base metal; parts thereof, of base metal, 83Metal; miscellaneous products of base metal
Machinery/Electrical	84 Machinery, 85 Electricals	84 Nuclear reactors, boilers, machinery and mechanical appliances; parts thereof, 85 Electrical machinery and equipment and parts thereof; sound recorders and reproducers; television image and sound recorders and reproducers, parts and accessories of such articles
Transport vectors and commodities	86 Railway/railway parts, 87 Vehicles/vehicle parts, 88 Aircraft/aircraft parts, 89 Ships/ships parts	86 Railway, tramway locomotives, rolling-stock and parts thereof; railway or tramway track fixtures and fittings and parts thereof; mechanical (including electro-mechanical) traffic signalling equipment of all kinds, 87 Vehicles; other than railway or tramway rolling stock, and parts and

		accessories thereof, 88 Aircraft, spacecraft and parts thereof, 89 Ships, boats and floating structures
Miscellaneous	67 Artificial flowers/feathers/wigs, 90 Miscellaneous instruments, 91 Clocks, 92 Musical instruments, 93 Arms/ammunition, 94 Furniture, 95 Toys, 96 Miscellaneous articles, 97 Artwork	67 Feathers and down, prepared; and articles made of feather or of down; artificial flowers; articles of human hair, 90 Optical, photographic, cinematographic, measuring, checking, medical or surgical instruments and apparatus; parts and accessories, 91 Clocks and watches and parts thereof, 92 Musical instruments; parts and accessories of such articles, 93 Arms and ammunition; parts and accessories thereof, 94 Furniture; bedding, mattresses, mattress supports, cushions and similar stuffed furnishings; lamps and lighting fittings, n.e.c.; illuminated signs, illuminated name-plates and the like; prefabricated buildings, 95 Toys, games and sports requisites; parts and accessories thereof, 96 Miscellaneous manufactured articles, 97 Works of art; collectors' pieces and antiques

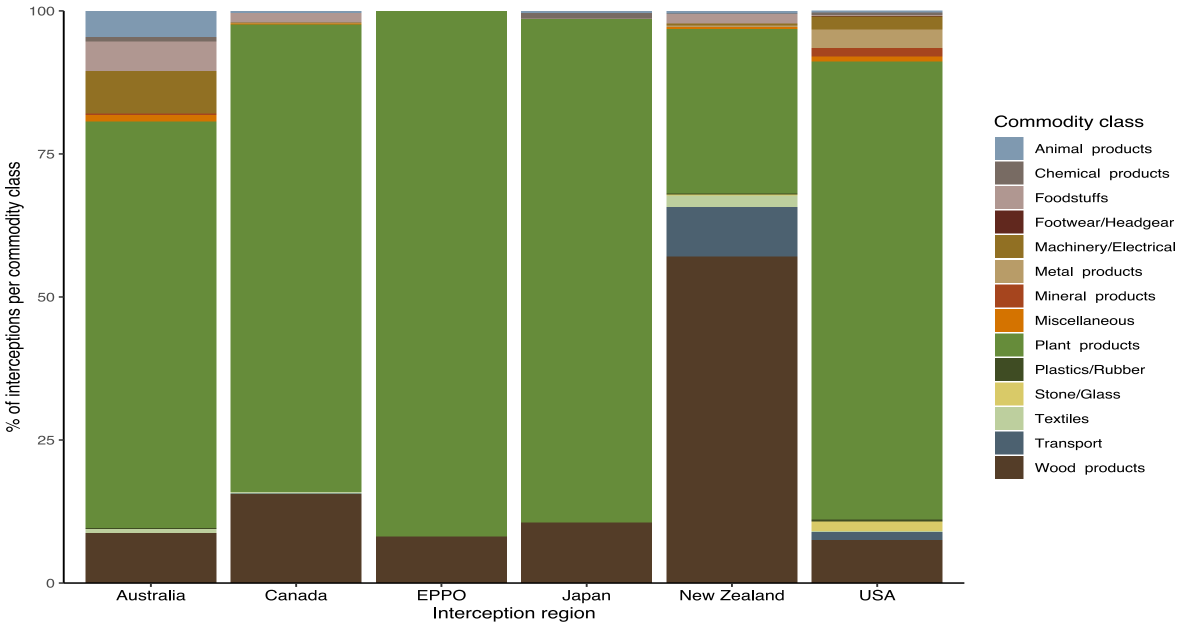
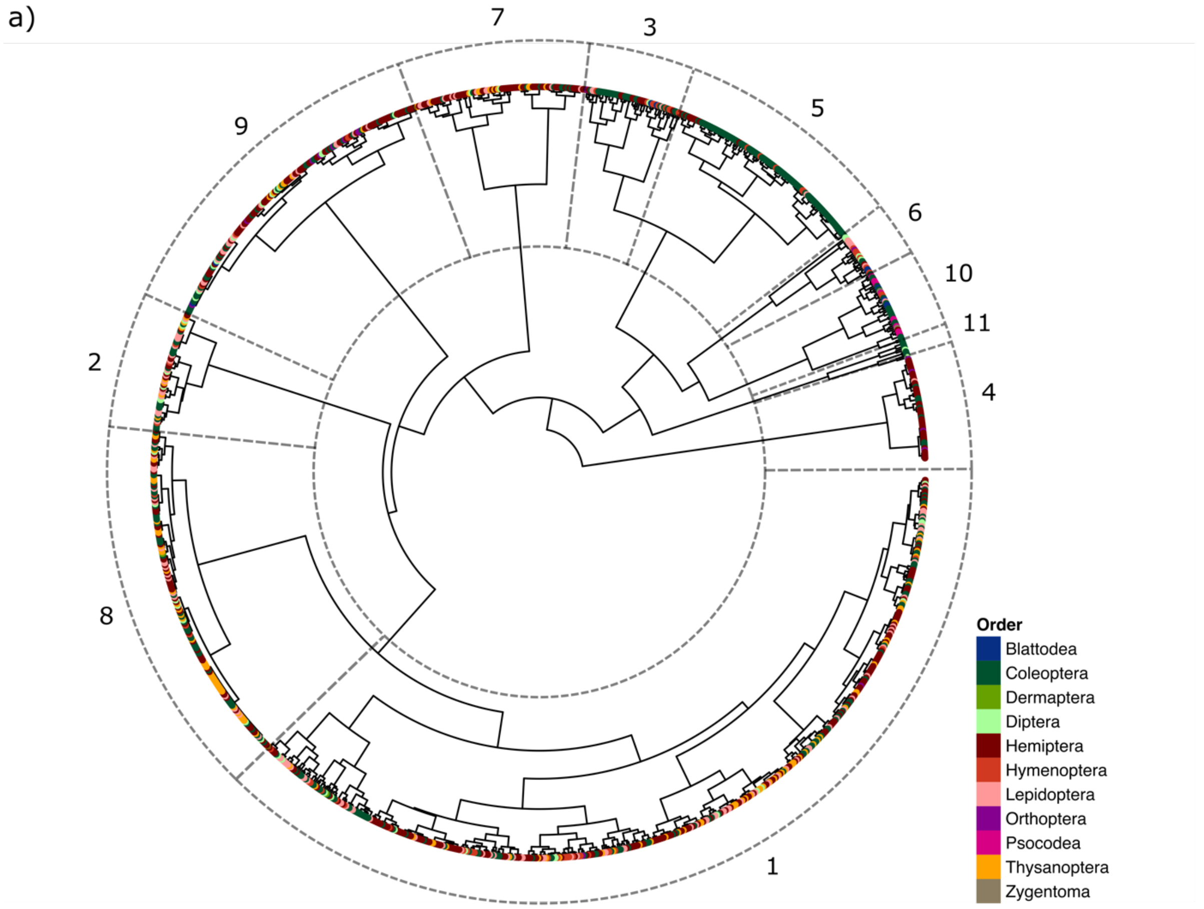


Figure S2. The proportion of interception events on each commodity class, in each of the six interception regions. The bars are coloured by the commodity class.



b)	1	2	3	4	5	6	7	8	9	10	11
Blattodea	0	0	2	0	0	2	0	0	2	4	0
Coleoptera	105	19	24	9	92	2	9	48	33	18	7
Dermaptera	1	0	0	0	0	0	0	1	0	0	0
Diptera	15	6	1	0	0	4	2	7	12	0	2
Hemiptera	185	11	10	39	9	1	55	54	78	1	0
Hymenoptera	27	3	10	0	5	7	0	3	4	2	0
Lepidoptera	73	18	3	1	1	6	11	21	18	1	0
Orthoptera	2	0	1	4	0	1	0	0	8	0	0
Psocodea	0	0	0	0	0	0	0	0	0	11	0
Thysanoptera	57	7	0	0	0	0	12	46	7	0	0
Zygentoma	0	0	0	0	0	0	0	0	0	2	0
Total	465	64	51	53	107	23	89	180	162	39	9

Figure S3. a) Hierarchical agglomerative clustering of species' commodity associations based on their coordinates in the CA. The leaves are coloured by the order each species belongs to, and the clusters are numbered and outlined with dashed lines. b) the number of species per order belonging to each cluster.

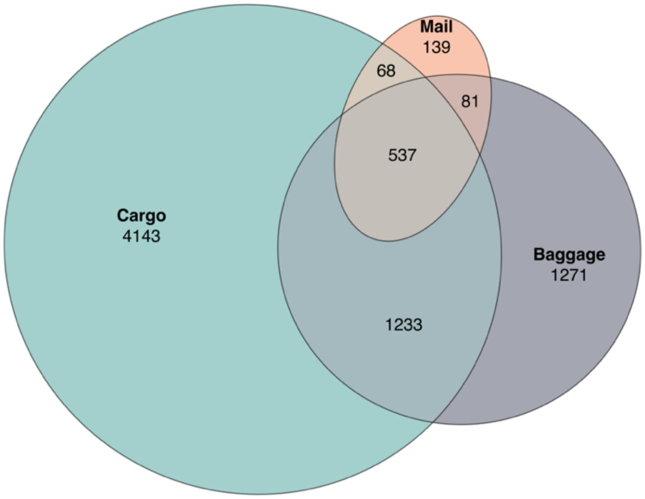


Figure S4. The number of species intercepted exclusively in cargo, in passenger baggage and in international mail, and the number of species intercepted in two, or all three pathways. The size of the circles is proportional to the number of species. The data is limited to the interceptions in Australia and the USA with information on the relevant pathway.

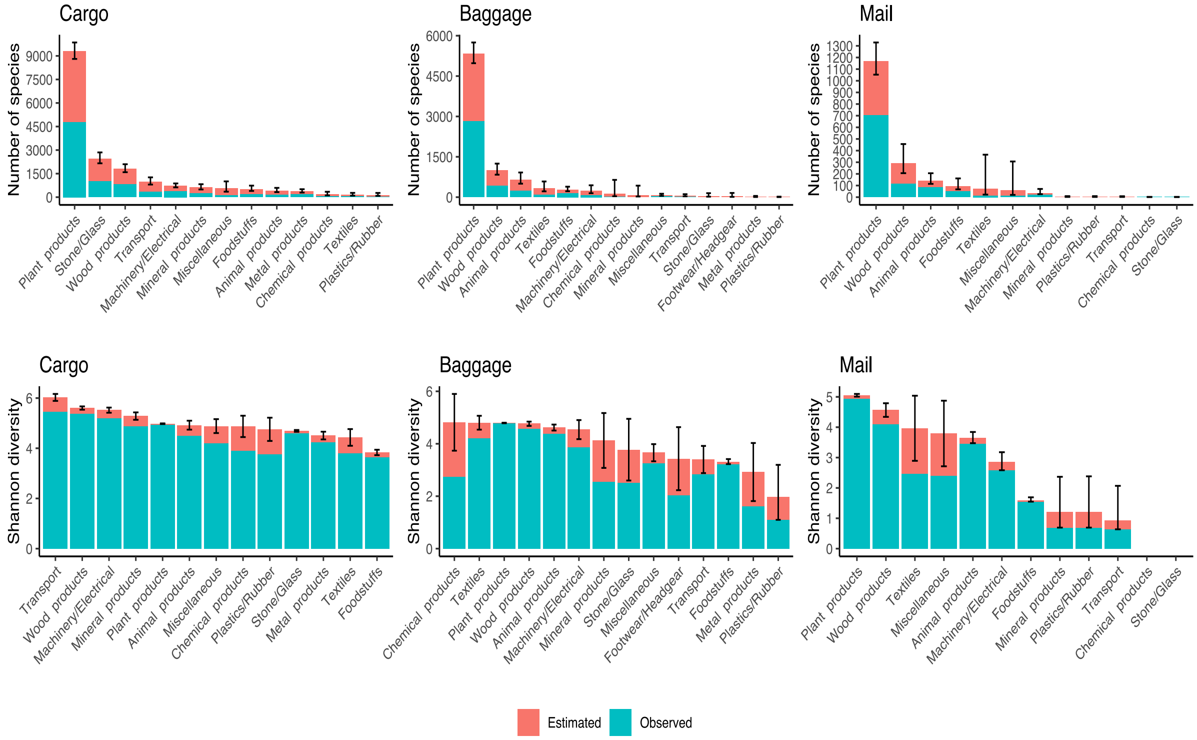


Figure S5. The observed (blue) and estimated (red) species richness and Shannon diversity transported with each commodity class in cargo, baggage and mail. The data is limited to the interceptions in Australia and the USA with information on the relevant pathway.

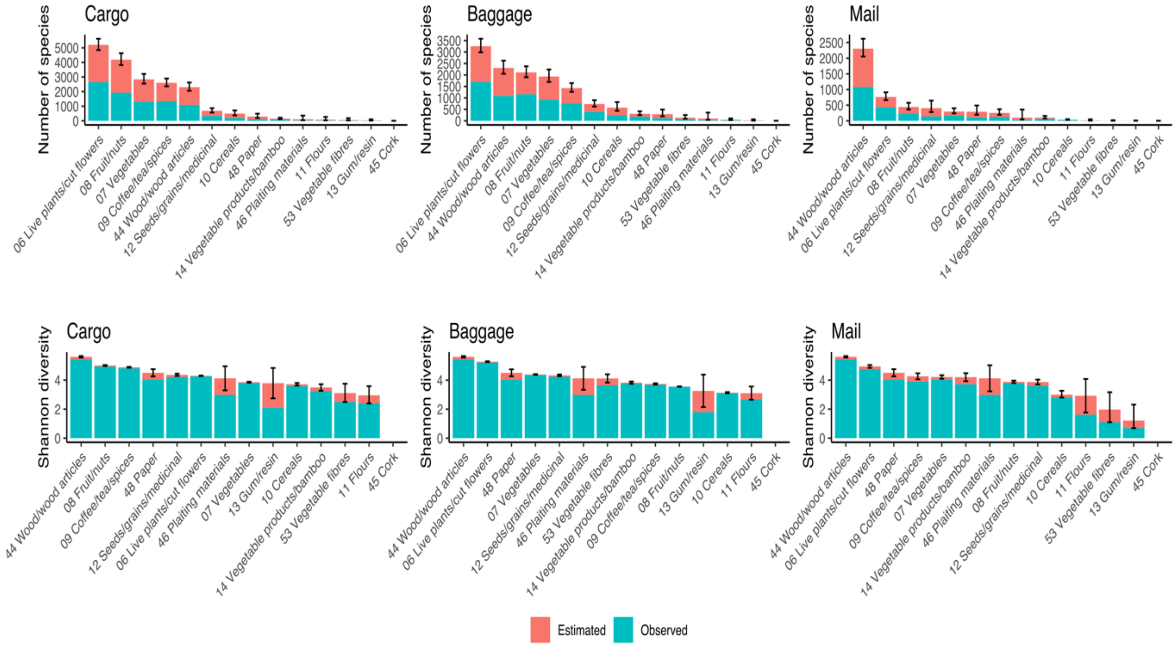


Figure S6. The observed (blue) and estimated (red) species richness and Shannon diversity transported with each HS-2 commodity group classed as plant products and wood products in cargo, baggage and mail. The data is limited to the interceptions in Australia and the USA with information on the relevant pathway.

Table S4. The percentage of variance in species' commodity associations explained by the order, the family and the genus they belong to, based on a series of CCAs (see methods section). P-values are adjusted for multiple hypothesis testing using the Bonferroni correction from the p.adjust() function in the 'stats' package (R Core Team, 2023).

Interception region	Variance explained by order	Variance explained by family	Variance explained by genus
Australia	16.1 %, $p = 0.02$	52.2 %, $p = 0.02$	74.6 %, $p = 0.02$
Canada	24.3 %, $p = 0.94$	69.8 %, $p = 0.04$	-
EPPO	35.9 %, $p = 0.02$	59.6 %, $p = 0.02$	55.6 %, $p = 0.18$
Japan	3.9 %, $p = 0.68$	18.1 %, $p = 1$	42.4, $p = 0.02$
New Zealand	26.4 %, $p = 0.02$	32.5 %, $p = 0.02$	59.7 %, $p = 0.02$
United States	6.6 %, $p = 0.02$	25.6 %, $p = 0.02$	62.1 %, $p = 0.02$
Pooled	6.7 %, $p = 0.02$	26 %, $p = 0.02$	44 %, $p = 0.02$

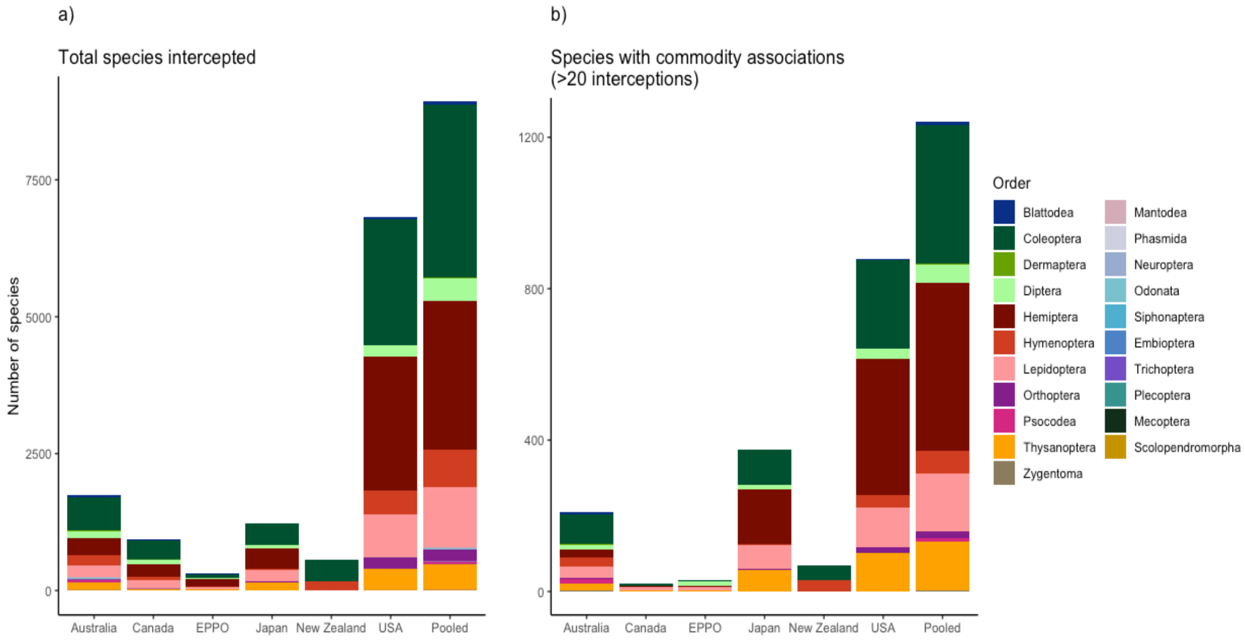


Figure S7. a) The total number of species, plus additional genera with no members identified to species level, intercepted in each region and in the pooled data, coloured by the order they belong to, and b) the number of species with more than 20 interceptions used to assess species' commodity associations in each region and in the pooled data, coloured by the order they belong to.

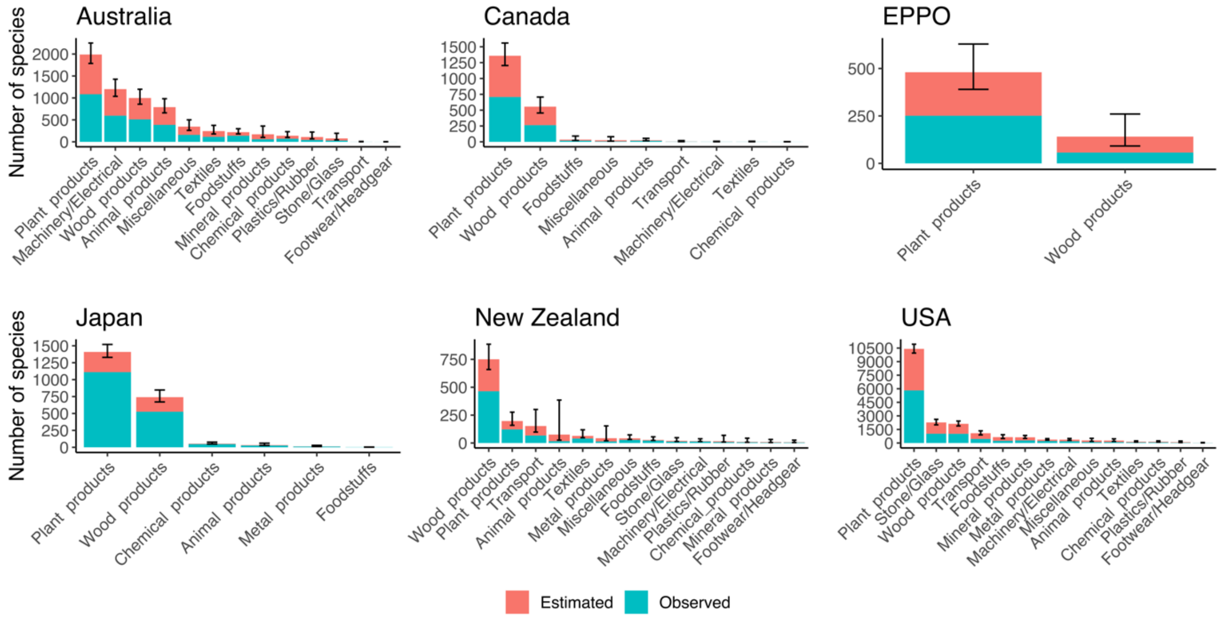


Figure S8. The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red) transported with each commodity class, in each interception region. The error bars indicate the standard error around the estimates of total richness.

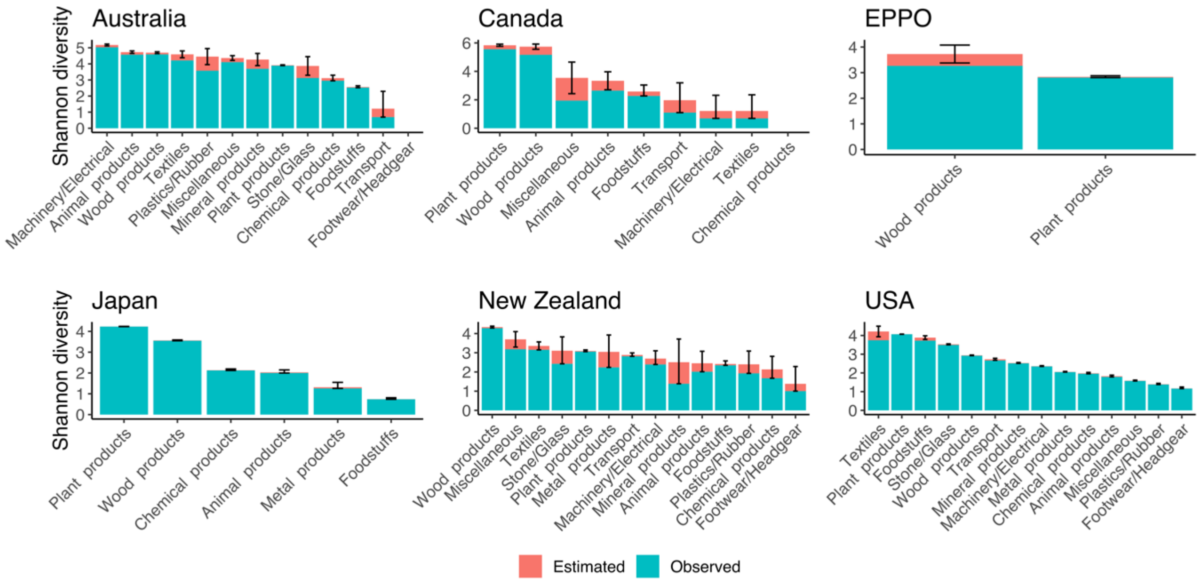


Figure S9. The observed Shannon diversity (blue) and Chao1 estimates of additional undetected diversity (red), transported with each commodity class, in each interception region. The error bars indicate the standard error around the estimates of total diversity.

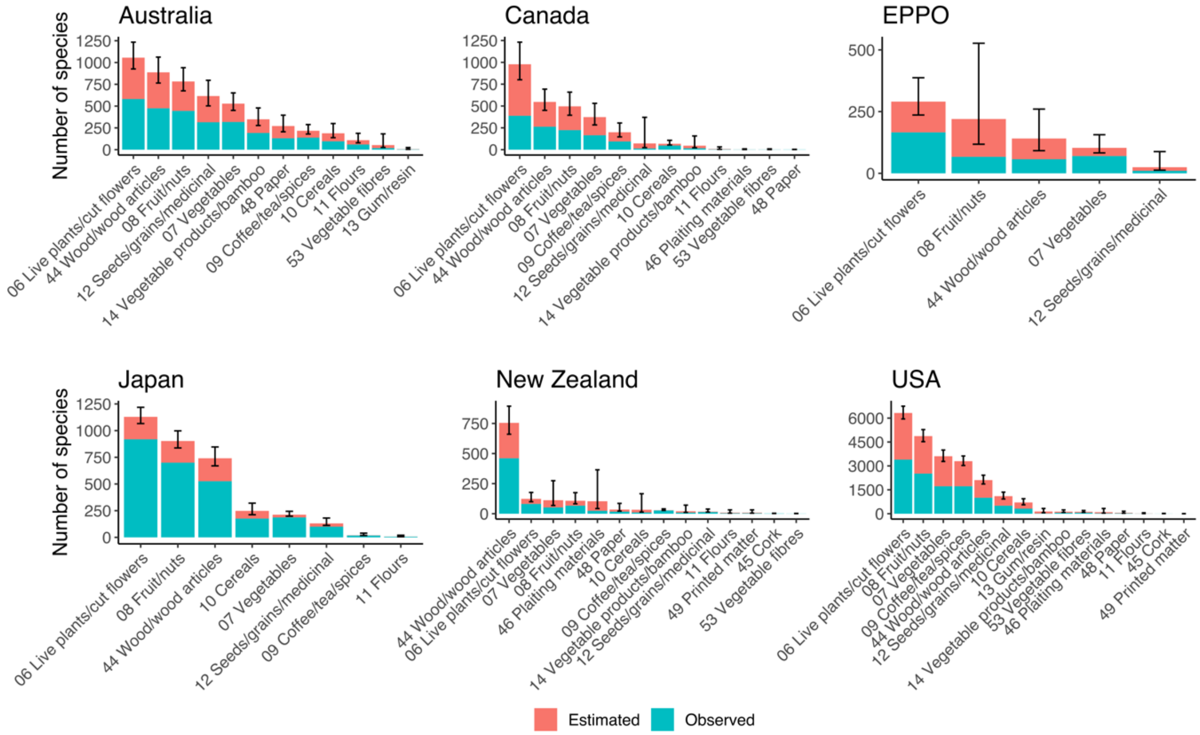


Figure S10. The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red) transported with each HS-2 commodity group classed as plant products and wood products, in each interception region. The error bars indicate the standard error around the estimates of total richness.

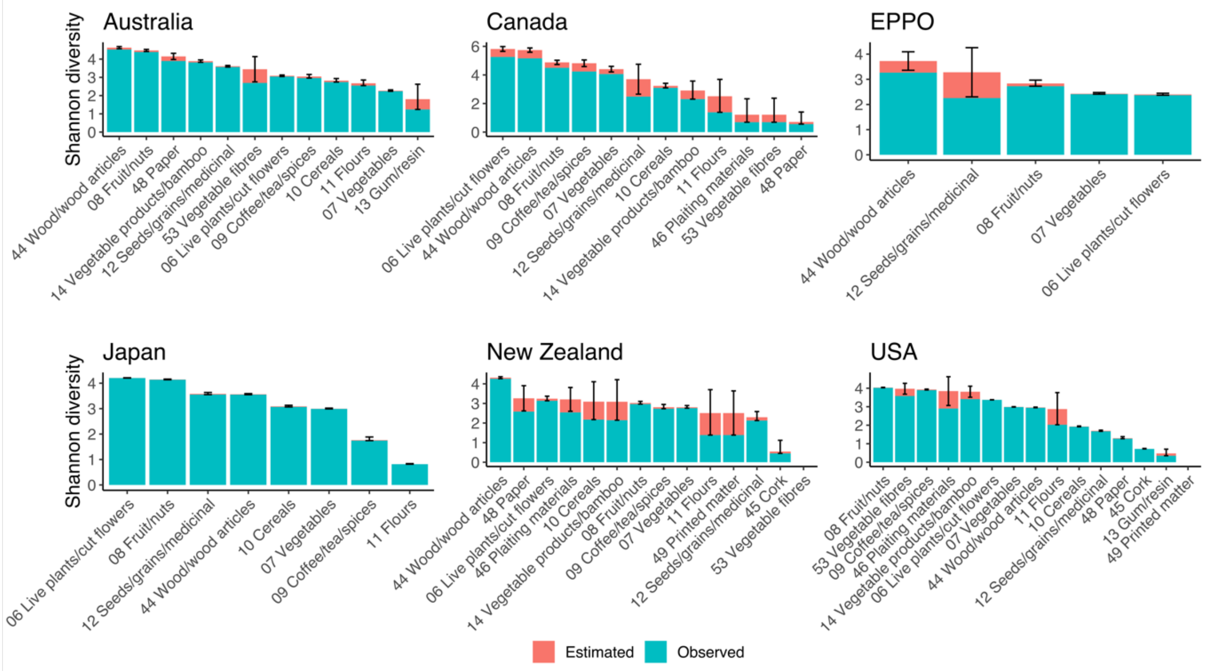


Figure S11. The observed Shannon diversity (blue) and Chao1 estimates of additional undetected diversity (red) transported with each HS-2 commodity group classed as plant products and wood products, in each interception region. The error bars indicate the standard error around the estimates of total diversity.

Chapter 2: Global flows of insect transport and establishment: the role of biogeography, trade, and regulations

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Author contributions: GFM curated and analysed the data with support from SO and CB. GFM and CB conceived the original idea. AML, HFN, DSP and TY curated and provided access to the interception records. OKB calculated climatic distance measures. All authors contributed to the design, discussed the results and contributed to the writing of the manuscript.

Abstract

Aim: Non-native species are part of almost every biological community worldwide, yet numbers of species establishments have an uneven global distribution. Asymmetrical exchanges of species between regions are likely influenced by a range of mechanisms, including propagule pressure, native species pools, environmental conditions, and biosecurity. While the importance of different mechanisms is likely to vary among invasion stages, those occurring prior to establishment (transport and introduction) are difficult to account for. We used records of unintentional insect introductions to test 1) whether insects from some biogeographic regions are more likely to be successful invaders, 2) whether the intensity of trade flows between regions determines how many species are intercepted and how many successfully establish, and 3) whether the variables driving successful transport and successful establishment differ.

Location: Canada, mainland USA, Hawaii, Japan, Australia, New Zealand, Great Britain, South Korea, South Africa.

Methods: To disentangle processes occurring during the transport and establishment stages, we analysed border interceptions of 8,199 insect species as a proxy for transported species flows, and lists of 2,076 established non-native insect species in eight areas. We investigated the influence of biogeographic variables, socio-economic variables, and biosecurity regulations on the size of species flows between regions.

Results: During transport, the largest species flows generally originated from the Nearctic, Panamaian and Neotropical regions. Insects native to eight of twelve biogeographic regions were able to establish, with the largest flows of established species on average coming from the Western Palearctic, Neotropical, and Australasian/Oceanian regions. Both the biogeographic region of origin and trade intensity significantly influenced the size of species flows between regions during transport and establishment. The transported species richness increased with Gross National Income in the source country, and decreased with geographic distance. More species were able to establish when introduced within their native biogeographic region.

Main conclusions: Our results suggest that accounting for processes occurring prior to establishment is crucial for understanding invasion asymmetry in insects, and quantifying regional biosecurity risks.

Keywords: *establishment, globalisation, human-mediated dispersal, insects, interceptions, invasion asymmetry, invasion stages.*

Introduction

The globalisation of trade and travel has led to an unprecedented acceleration of species introductions (Seebens *et al.*, 2017; Bonnamour, Gippet and Bertelsmeier, 2021), which is increasingly impacting native ecosystems and human societies (Pagad *et al.*, 2015). Mapping non-native species diversity and exchanges between world regions is therefore key to understanding large-scale drivers of invasions and identifying regionally specific biosecurity risks. Extensive and spatially explicit databases (e.g., CABI Invasive Species Compendium (CABI, 2022); DAISIE (Delivering Alien Invasive Species Inventories for Europe) (Roy *et al.*, 2020)) are increasingly available to document non-native species distributions, and there have been considerable advances in describing regional invasion patterns (e.g., van Kleunen *et al.*, 2015; Capinha *et al.*, 2017; Casado *et al.*, 2018). Other studies have focussed on the characteristics of trade and travel network topologies driving human-mediated dispersal (Tatem, 2009; Banks *et al.*, 2015), or have identified socio-economic and biogeographic variables that are linked to non-native species richness (Baiocchi and Dalmazzone, 2000; Capinha *et al.*, 2017; Dawson *et al.*, 2017; Lantschner, Corley and Liebhold, 2020). Yet while non-native species have been recorded in almost every biological community around the world (Convention on Biological Diversity, 2001), species establishments outside of their native range are not evenly distributed geographically. The imbalance in species exchanges, with some regions over- or under-represented as donors and recipients, is referred to as 'invasion asymmetry' (Torchin *et al.*, 2021). For example, many non-native plants in the Southern hemisphere have originated in the Northern hemisphere, while the opposite trend is not observed (van Kleunen *et al.*, 2015).

Different mechanisms have been proposed to explain invasion asymmetry (Figure 1), often focussing on environmental factors and biotic acceptance or resistance during establishment (Jeschke and Genovesi, 2011). However, biological invasions are composed of a series of sequential stages: transport, introduction, establishment, and subsequent spread (Blackburn *et al.*, 2011; Gippet *et al.*, 2019) (Figure 1). Each stage constitutes a barrier that must be overcome for a species or population to successfully establish and proliferate. The overall invasion success of a species is accordingly determined by the extent to which its individuals or propagules can overcome these barriers (Blackburn *et al*., 2011). The number of individuals introduced or the number of introduction events (hereafter propagule pressure; Williamson, 1996; Lockwood, Cassey and Blackburn, 2005) is a key element in species invasion success or failure. However, previous work has often not considered that the mechanisms responsible for differential invasion success, often linked to species traits, are likely to vary considerably throughout the invasion process (Blackburn *et al*., 2011; Gippet *et al*., 2019). While it has been possible to control for the introduction stage in rare cases where release attempts are well-recorded (birds: Blackburn, Cassey and Lockwood, 2008; Chiron, Shirley and Kark, 2009; mammals: Jeschke and Genovesi, 2011), in most previous analyses of invasion patterns it has not been possible to isolate the factors responsible for invasion success at each stage (Puth and Post, 2005). Consequently, our understanding of species richness introduced from a source region to a destination region, hereafter referred to as species flows, is largely based on the distribution of already established non-natives (e.g., Capinha *et al*., 2015; van Kleunen *et al*., 2015; Dawson *et al*., 2017), hindering our ability to separate ecological factors from the influence of introduction pressure.

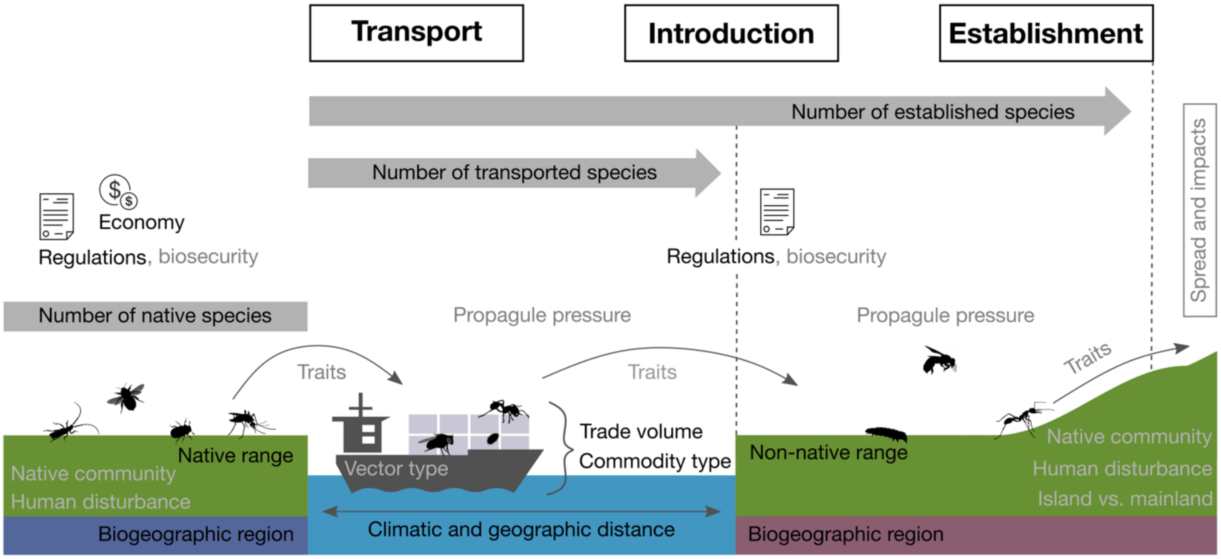

Figure 1. The invasion process for unintentional species introductions. The stages of transport, introduction and establishment are shown, along with key mechanisms affecting success/failure at each stage. Transport includes both maritime, aerial and overland introduction pathways. We have not included secondary, bridgehead introductions. Mechanisms and stages not explicitly

included in our analyses are shown in grey. The dotted lines indicate the two points we analysed data from; border interceptions after transport, and lists of established insects. Adapted from Schulz et al. (2019).

In this study, we address key mechanisms determining the number of non-native species exchanged between regions at the transport stage, and after establishment. Firstly, regions differ in the size of the native species pool potentially available for transport (Liebhold, Brockerhoff and Kimberley, 2017; Seebens *et al.*, 2018). The pool of species in an area thereby sets an upper limit for the number of non-natives that area can supply. Furthermore, the environmental conditions species are adapted to also vary regionally, and likely play a role in establishment success outside their native range (Bomford *et al.*, 2009; Cunze *et al.*, 2018). Secondly, invasion asymmetry can arise from differences in propagule pressure, or the number of species introduced (colonization pressure; Lockwood, Cassey and Blackburn, 2009; Blackburn, Cassey and Duncan, 2020). Propagule- and colonization pressure have been identified as key drivers of invasion success for several taxa (Lockwood, Cassey and Blackburn, 2005; Blackburn, Cassey and Duncan, 2020), and are tightly linked to human activities (Pyšek *et al.*, 2010). As most introductions occur via human-mediated dispersal (Hulme *et al.*, 2008), the spatial and temporal heterogeneity of global trade and transport networks is likely a key contributor to invasion asymmetry (De Benedictis and Tajoli, 2011; Banks *et al.*, 2015). Lastly, many countries put significant efforts into preventing invasions (Saccaggi *et al.*, 2016; Black and Bartlett, 2020). Biosecurity measures that exclude new species introductions are generally considered more efficient than managing already established populations (Leung *et al.*, 2002), and are coordinated through national policies and international conventions. Nonetheless, resources to regulate non-native species are also unevenly distributed, potentially exacerbating invasion asymmetry (McGeoch *et al.*, 2010; Bacon, Bacher and Aebi, 2012; Early *et al.*, 2016).

To disentangle the processes occurring during transport and establishment, we analysed insect border interception records (transport stage) and country-level lists of established non-native insects (establishment stage). Border interceptions generally represent live insects that have been successfully transported, and as such can be considered as a proxy for introductions. Insects are among the most widespread and damaging non-native species in terrestrial habitats, costing at least 70 billion US $ annually (Bradshaw *et al.*, 2016; Lovett *et al.*, 2016). Due to their small size, they are easily transported accidentally through human activities (Meurisse *et al.*, 2019). While the introduction pathways of established species remain poorly known (National Research Council, 2002), insects are the focus of considerable biosecurity efforts globally (Leung *et al.*, 2002; Lance, Woods and Stefan, 2014; Nahrung *et al.*, 2022). In addition to growing inventories of established non-native species, many countries record insect species detected during inspections of trade goods, mail and personal baggage at ports of entry (i.e., land borders, air- and sea-ports and transitional facilities) as part of national biosecurity programmes (Saccaggi *et al.*, 2016; Black and Bartlett, 2020)**.** These border interceptions offer insight into the largely unobserved processes occurring prior to unintentional introductions (Turner *et al.*, 2021).

We quantified flows of transported species based on interceptions of 8,199 insect species arriving in Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain, and South Africa, from 227 countries around the world. Lists of 2,076 established non-native insects, along with records of their native biogeographic region, allowed us to quantify flows of established species to the same destinations, plus Australia and South Korea. We modelled the effects of biogeography, trade intensity and biosecurity efforts on flows of insect species among regions, allowing us to test 1) whether insects from some biogeographic regions are more likely to be successful invaders, 2) whether the intensity of trade flows between regions determines how many insect species are intercepted and how many successfully establish, and 3) whether the variables driving successful transport and successful establishment differ.

Methods

Flows of transported species

We analysed border interception records from Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain, and South Africa to quantify the flows of insect species arriving from countries worldwide. See Table S1 for a description of the interception records available from each destination. The data consist of records of insect species detected during inspections of international cargo, mail, vessels, and passenger baggage at air, land, and maritime ports of entry. These border interceptions represent a fraction of the total insects being transported. While interceptions can be considered a proxy for species' undetected arrival, they do not directly represent introductions (Turner *et al*., 2021). Furthermore, different types of organisms differ in the probability that they will be detected and recorded during inspection. We only included records with information on the source country and the associated commodity, and where the intercepted insect was identified to the species level (56 %). We counted any genera with no members identified to species level as representing one additional species. We standardized insect taxonomic names across years and recording regions according to the Global Biodiversity Information Facility (GBIF) backbone taxonomy (GBIF Secretariat, 2019) using the 'taxize' (Chamberlain and Szöcs, 2013) and 'rgbif' R packages (Chamberlain *et al*., 2021)**. T**his process was largely automated, but a small proportion of synonyms may still be present**.** We analysed interceptions between 1960 and 2019, depending on their availability per country (see Table S1). We carried out all analyses at a decadal scale to capture changing trade patterns while limiting the influence of random yearly fluctuations.

Flows of established species

We used comprehensive lists of established non-native insect species in Australia, New Zealand, Great Britain, Japan, North America (continental USA and Canada), Hawaiian Islands, South Korea, and South Africa. The native biogeographic region was recorded for each species using Holt's system (see below). The species lists and main source references are available from Turner, Blake and Liebhold (2021). We did not include species that were intentionally introduced in our analyses. Furthermore, non-native populations often become the source of secondary introductions through a process termed the 'bridgehead effect' (Lombaert *et al*., 2010; Bertelsmeier and Ollier, 2021). To increase the likelihood that species arrived directly from their native region rather than via already invaded areas elsewhere, we excluded any species established in, or native to more than one biogeographic region. We restricted our analyses to first records of species establishment from 1960 onwards when detailed import values are available by commodity.

Socio-economic factors

There is ample evidence linking biological invasions to trade, and broad metrics of economic activity such as Gross Domestic Product (GDP) have been used to predict invasion success in several previous studies (e.g., Baiocchi and Dalmazzone, 2000; Sharma, Esler and Blignaut, 2010; Dawson *et al*., 2017). However, Gross National Income (GNI) represents total income, whether earned within a country's borders or derived from foreign investments, and may provide a better measure of countries' economic condition (Maverick, 2022). Measures of GDP (constant 2015 USD) and GNI (constant 2015 USD) from World Bank and OECD National Accounts data were highly correlated, so we used yearly GNI per capita (The World Bank Group, 2022), summed per decade to quantify the economic status of each source country.

We standardised commodity descriptions in the interception records using the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods (World Customs Organization, 2021), and subsequently grouped commodities into broad classes based on the type of product (see Table S2). To provide a precise measure of relevant trade flows, we used the 'tradestatistics' R package (Vargas, 2022) to access historical import values per commodity based on UN Comtrade data (United Nations, 2022). Additional import records for Hawaii were obtained from the US Census Bureau as imports to the district of Honolulu (United States Census Bureau, 2022). We summed yearly import values in US dollars for each combination of commodity class, source country and destination, per decade. The dollar value of imports was corrected for inflation using the ots_gdp_deflator_adjustment() function in the 'tradestatistics' package with 2018 as the reference year.

While we know the exact year when species were intercepted, there is commonly a lag time between a species' establishment and its detection (Kowarick, 1995; Sakai *et al*., 2001). Such discovery lags for plant invasions sometimes exceed 50 years (Kowarick, 1995; Aikio, Duncan and Hulme, 2010; Larkin, 2012), but may be shorter for animals (Essl *et al*., 2011; Aagaard and Lockwood, 2014). In Japan, non-native insects generally have a lag time of 4-10 years before detection (Kiritani and Yamamura, 2003). Consequently, we used import values in the same decade as establishment to predict variation in species richness.

Biogeographic regions

To describe insect invasion asymmetry between regions, we assigned all source countries and destinations to biogeographic regions. The regions were classified as per Holt *et al*. (2013), with the large Palearctic region divided into the Eastern and the Western Palearctic (supplementary

Figure S1). Due to the low sample size, we excluded flows from the Antarctic and Madagascan biogeographic regions and combined the Australasian and Oceanian regions in our analyses.

Climatic and geographic distance

While environmental similarity between the source and destination may be of limited importance during the early stages of the invasion process, it is likely to have a strong impact on establishment success (Bomford *et al.*, 2009; Cunze *et al.*, 2018). We quantified the climatic similarity between countries using the 19 bioclimatic variables from the WorldClim Global Climate Database at a resolution of 5 arc-minutes (Hijmans *et al.*, 2005). The bioclimatic variables were reduced to eight axes using Principle Components Analysis (PCA) using the dudi.pca() function from the ade4 package (Dray and Dufour, 2007), then grouped based on the 32 Köppen-Geiger climate categories (Kottek *et al.*, 2006). For each Köppen-Geiger climate, the eight PCA axes representing bioclimatic conditions were projected into hypervolume space using the Gaussian method, with a chunk size of 500 in the 'hypervolume' package (Blonder *et al.*, 2014). We calculated the Euclidian distance between the centroids of each climate in hypervolume space using the dis_centroid() function (Blonder *et al.*, 2014). We then used a double PCA to create a dissimilarity matrix of how frequently each Köppen-Geiger climate occurs per country based on these distances. The values were normalised so that 0 represents no dissimilarity between regions, and 1 represents complete dissimilarity.

In addition to climatic distance, the geographic distance transported may have an impact on introduction success if species more easily survive transport across short distances (Seebens, Gastner and Blasius, 2013; Chapman *et al.*, 2017). We used a vector map of country boundaries from the 'rworldmap' package with the WGS 84 coordinate reference system (South, 2011), and calculated the geographic distance transported as the distance in kilometres between country centroids. We calculated country centroids using the gCentroid() function in the 'rgeos' package (Bivand and Rundel, 2021) and the great circle distances between them using the st_distance() function in the 'sf' package (Pebesma, 2018).

Native insect richness

Species that are transported from an area are necessarily a subset of the pool of species present there. While regional variation in species richness and diversity is therefore likely important for invasion asymmetry, insect biodiversity remains poorly quantified in many parts of the world. Stork *et al*. (2015) estimate that there are 5.5 million insect species globally. The distribution of Formicidae is well documented compared to most other insect taxa, so to estimate the species pool potentially available for transport in each source country, we divided 5.5 million by the proportion of native ant species present in that country using data from Global Ant Biodiversity Informatics database (Guénard, 2017). This follows the method used by Stork (2018) to estimate the number of insect species per biogeographic region. The number of native vascular plants per country based on the World Checklist of Vascular Plants (Govaerts *et al*., 2021) was highly correlated with our estimates of insect species richness (Pearson's r = 0.84), so we used the latter to quantify the size of the native species pools available for transport.

Biosecurity regulations

National biosecurity programs direct considerable efforts towards preventing insect invasions through extensive pre-border measures (Sequeira and Griffin, 2014). As a proxy for biosecurity efforts, we used the number of international treaties, regulations, and legislation (referred to as regulations from here on) relevant to invasive species that a country is a member of. The number of regulations was based on the ECOLEX database, as per Turbelin, Malamud and Francis (2017). ECOLEX consolidates information on global environmental law, including international treaties, national legislation, and technical guidance documents (FAO, IUCN, UNEP, 2016).

Statistical modelling

Flows of transported species

A 'flow' here represents the species richness associated with a specific source country and destination pair, the commodity class insects arrived with, and the decade when insects were intercepted. Because interception data only records positive detections (they do not record absences), these data are inherently zero-truncated. Therefore, insect flows during transport were modelled using a generalized linear mixed model (glmm) with a zero-truncated negative binomial distribution from the 'glmmTMB' package (Brooks *et al*., 2017). We also considered a zero-truncated Poisson model to represent the counts of species but based on model AIC the zero-truncated negative binomial model provided a better fit. The model included the variables in Table 1, as well as an interaction term between the import value and commodity class in the model, as the effect of trade intensity may differ between commodities. We included the decade of interception as a random effect to account for variation over time. There are differences in inspection methods, targets, and efforts, as well as in trade patterns depending on the partners involved, so we also included the source country, the destination, and the source-destination pair as random effects.

Flows of established species

A 'flow' here represents the number of species from a specific biogeographic region of origin that have established in a specific destination, per decade. We do not have information on the exact introduction pathway for most established species, but as plant products are the main commodities associated with insect movements through trade (Liebhold *et al*., 2012; Meurisse *et al*., 2019; Fenn-Moltu *et al*., 2022) we used the US dollar value of plant products imported to represent trade intensity. We assessed other trade metrics including total commodity import values, imports of agricultural commodities and imports of plant and wood products, as well as these values for the preceding decade, but plant product imports in the same decade was the best fit based on model AIC. We again used a glmm with a zero-truncated negative binomial distribution to predict the species richness per flow (Table 2). We included the decade in which a species established, and the area in which it established as random effects to account for variation in detectability and establishments over time and between destinations. We used the Anova() function in the 'car' package (Fox and Weisberg, 2018) to compute analysis-of-variance tables using type II Wald chi square tests for both models. All analyses were conducted in R (R Core Team, 2017).

Results

8,199 insect species were intercepted from 227 countries across all biogeographic regions (Figure 2). Insects were intercepted arriving with 14 different commodity classes. During transport, the species richness per flow ranged from 1 to 967 species, with a median of three. The full output of the model predicting flow size during transport is in Table S4. A total of 3,994 species had established in the eight destinations we considered, encompassing insects native to the Afrotropical, Eastern and Western Palearctic, Sino-Japanese, Neotropical, Nearctic, Oceanian and Australasian regions (Figure 2). The decade when establishment was first recorded was available for 2,076 of these species. The species richness per flow of established insects ranged from 1 to 107 species, with a median of three. The full output of the model predicting flow size of established species is in Table S5.

Table 1. The variables included in the model of species flows during transport, along with their description and the type of variable they represent.

Variable	Description	Type
Species richness	Number of insect species intercepted per flow (unique combination of source country / destination * commodity class * decade)	Response
Import value	Log value imported per flow in US dollars	Explanatory
Commodity class	Identity of 14 broad commodity classes that insects were intercepted with (e.g., plant products, machinery, or stone/glass)	Explanatory
Biogeographic region	Biogeographic region the insects arrived from	Explanatory
Source species pool	Estimated number of native insect species in the source country	Explanatory
Regulations per source country	Number of regulations relating to invasive species the source country is a member of, ranging from 0-30	Explanatory
Regulations per destination country	Number of regulations relating to invasive species the destination country is a member of, ranging from 12-21	Explanatory
Gross National Income (GNI)	Log GNI per capita for the source country in constant 2015 US dollars	Explanatory
Geographic distance	Distance in km between the source and destination country centroids	Explanatory
Climatic dissimilarity	Climatic dissimilarity between the source and destination country, ranging from 0 (no dissimilarity) to 1 (complete dissimilarity)	Explanatory
Within or between regions	Whether species are transported within the same biogeographic region (intra) or not (inter)	Explanatory
Source	Which country intercepted species arrived from	Random

Destination	Area where species were intercepted; either Australia, New Zealand, Great Britain, mainland USA, Hawaii, Japan, or South Africa	Random
Source and destination area	Specific combination of source and destination areas the insects are transported between	Random
Decade	Decade of port interception	Random

Table 2. The variables included in the model of established species flows, along with their description and the type of variable they represent.

Variable	**Description**	**Type**
Species richness	Number of established insect species per flow (unique combination of native region * destination * decade)	Response
Import value	Log value of plant products imported per flow in US dollars	Explanatory
Biogeographic region	Biogeographic region the established insects are native to	Explanatory
Regulations per destination	Number of regulations relating to invasive species the destination country is a member of, ranging from 12-24	Explanatory
Within or between regions	Whether species have established within their native biogeographic region (intra) or not (inter)	Explanatory
Destination area	Area where insects have established; either Australia, Great Britain, Hawaii, Japan, New Zealand, North America (continental USA and Canada), or South Korea	Random
Decade	Decade of establishment first record	Random

<u>1) Are insects from some biogeographic regions more likely to be successful invaders?</u>

Interception records from the seven destinations analysed in this study documented the transport of a total of 2,490 insect species from the Panamaian region, 2,376 from the Nearctic, 2,283 from the Western Palearctic, 2,104 from the Neotropical, 1691 from the Oriental, 1,090 from the Afrotropical, 1,069 from the Sino-Japanese, 894 from the Saharo-Arabian, 668 from the Australasian, 464 from the Eastern Palearctic, 330 from the Oceanian, 31 from the Madagascan region, and 1 species from the Antarctic region. On average, the greatest species richness per flow originated from the Nearctic (mean of 31.1 species, SD = 114), Panamaian (mean 21.8, SD

75.9) and Neotropical regions (mean 15.5, SD 60.8) at the transport stage. In the eight destinations where we had lists of non-native insects, 1,482 Western Palearctic species had established, along with 561 Australasian, 512 Neotropical, 394 Nearctic, 365 Sino-Japanese, 298 Eastern Palearctic, 263 Oceanian species, and 119 Afrotropical species. The mean species richness per flow was greatest from the Western Palearctic (mean of 18.4 species, SD 20.3), Neotropical (mean 11.4, SD 20.4) and Australasian plus Oceanian region (mean 8.5, SD 12.3).

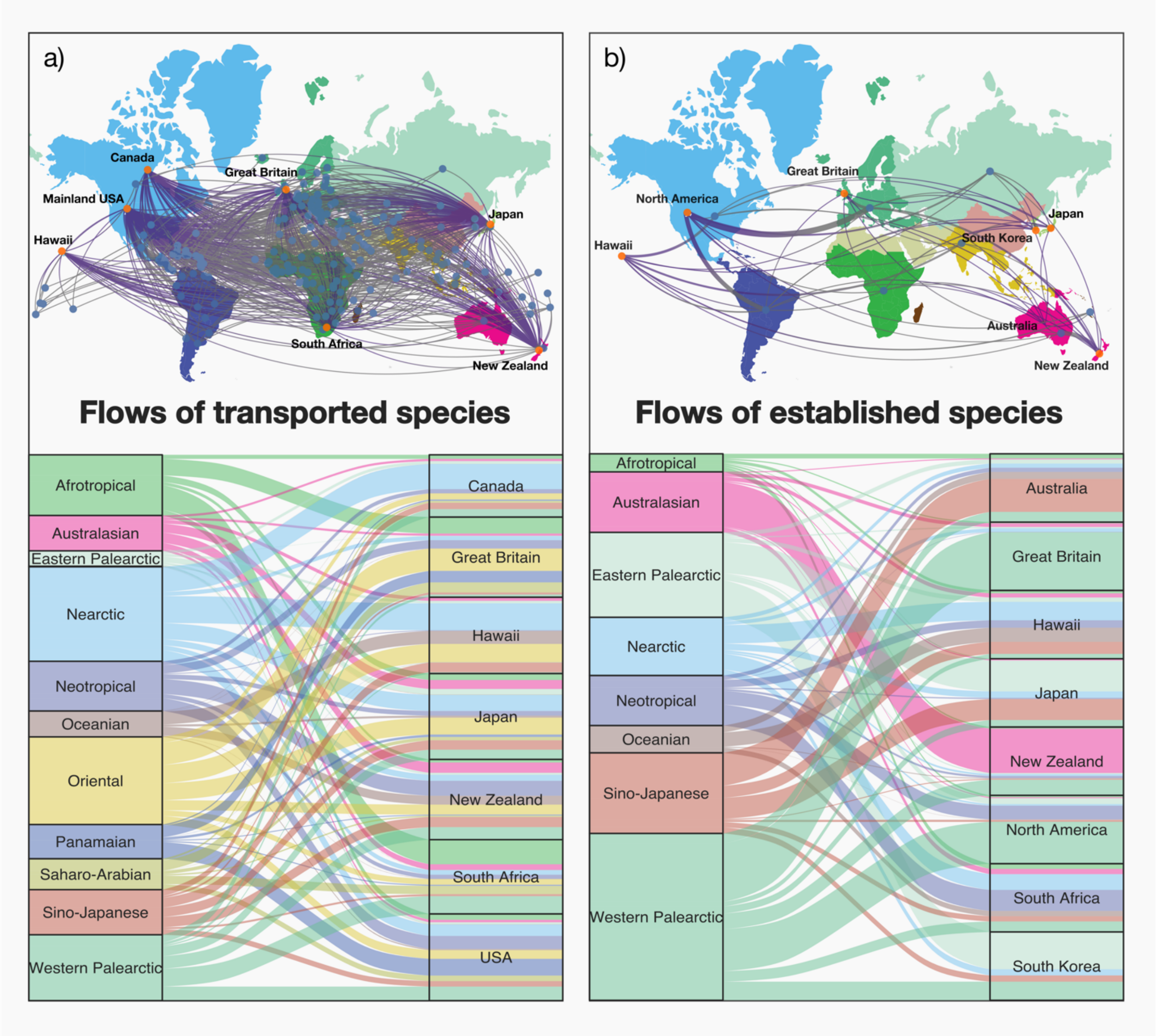

Figure 2. Flows of (a) transported and (b) established insect species. The maps show the geographical location of the flows analysed, and the links are proportional to the size of the flows. The alluvial plots show the percentage of species arriving in each destination from each biogeographic region of origin. In the alluvial chart (a) small flows from the Madagascan and Antarctic regions are not labelled.

During the transport stage (assessed using interceptions), the species richness per flow varied significantly depending on the biogeographic region of origin ($\chi^2 = 29.32$, $p < 0.001$) (Figure 3), and decreased significantly with geographic distance ($\chi^2 = 10.43$, $p = 0.001$). The number of established species also varied significantly depending on their native biogeographic region ($\chi^2 = 410.10$, $p < 0.001$).

Larger pools of native species in the source country led to a marginally significant increase in species richness per flow during transport ($\chi^2 = 3.48$, $p = 0.06$). We lack the precise information on species' native ranges needed to test the effect of species pools on flows of established insects, but neither species richness per flow nor the total number of established species were correlated with species richness in the native region (supplementary Table S3). For example, the greatest number of established species originated from the two Palearctic regions, which together only comprise the fifth-largest pool of native insect species.

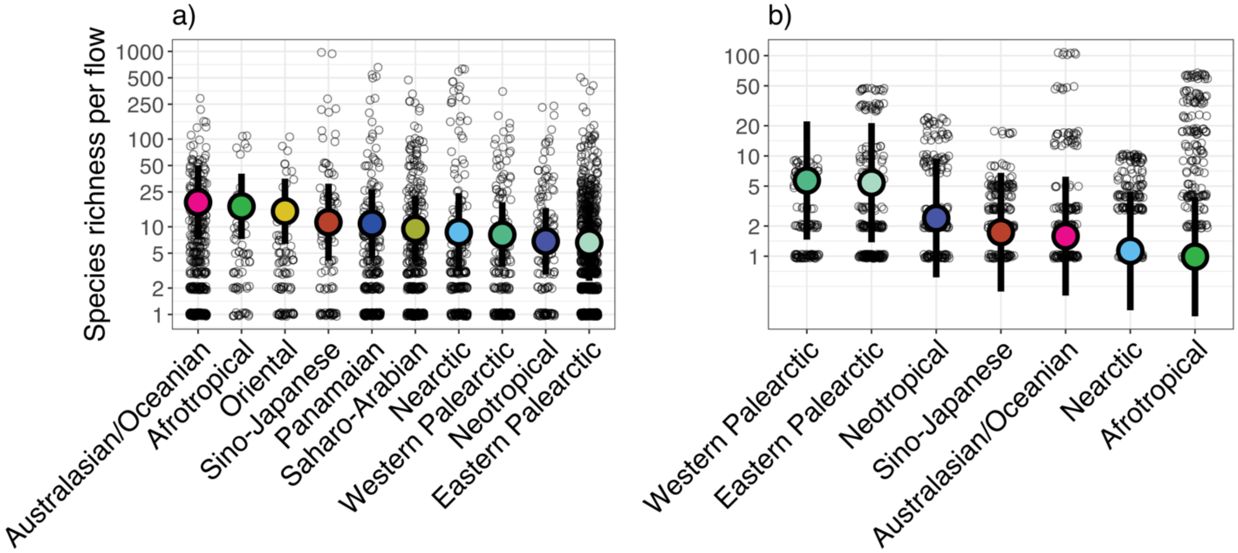

Figure 3. The species richness per flow depends on the biogeographic region of origin for (a) intercepted species and (b) established insect species. The grey circles represent individual flows (unique combinations of source/destination * commodity class * decade intercepted), and the coloured circles show model predictions using the ggpredict() function from the 'ggeffects'

package (Lüdecke, 2018). The error bars are 95 % confidence intervals. The x-axis has been log transformed for readability.

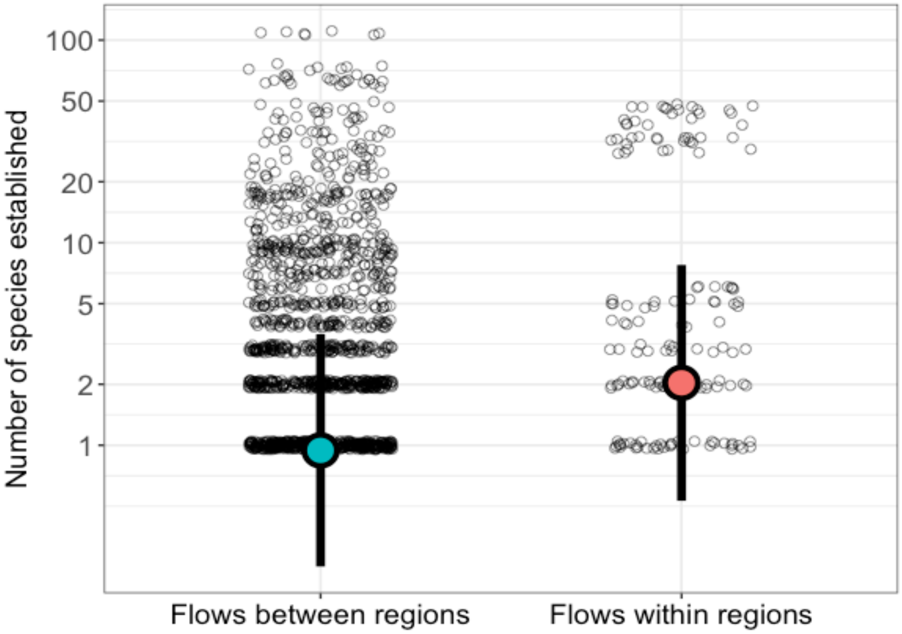

Figure 5. Species richness per flow of established insect species, when introduced between biogeographic regions (blue) or within their native biogeographic region (red). The grey circles represent individual flows (unique combinations of native biogeographic region * destination * decade established), and the coloured circles show model predictions using the ggpredict() function from the 'ggeffects' package (Lüdecke, 2018). Error bars are 95 % confidence intervals. The x-axis has been log transformed for readability.

<u>2) Does the intensity of trade flows between regions determine how many insect species are intercepted and how many successfully establish?</u>

Greater import values were associated with significantly more species intercepted during transport ($\chi^2 = 137.48$, $p < 0.001$), as was a higher GNI in the source country ($\chi^2 = 19.04$, $p < 0.001$) (Figure 5). As expected based on previous studies (e.g., Kenis *et al.*, 2007; Liebhold *et al.*, 2012; Suhr *et al.*, 2019; Fenn-Moltu *et al.*, 2022; Ollier and Bertelsmeier, 2022), the species richness intercepted also depended on the commodity class ($\chi^2 = 2391.74$, $p < 0.001$). Greater plant product import values were associated with more established species per flow ($\chi^2 = 246.26$, $p < 0.001$).

3) Do the variables driving successful transport and successful establishment differ?

Due to the lack of fine-scale spatial information on species' native ranges in our data, we could not directly compare many variables between transport and establishment (i.e., climatic distance, geographic distance, GNI of the source country, native species pool size, or regulatory efforts in the source country). The species richness transported did not decrease significantly with either the number of regulations in the destination ($\chi^2 = 1.74$, $p = 0.187$), or the source country ($\chi^2 = 0.07$, $p = 0.789$). We could only test the effect of regulations in the destination country for established species flows, but there was no significant effect at this stage either ($\chi^2 = 0.21$, $p = 0.643$).

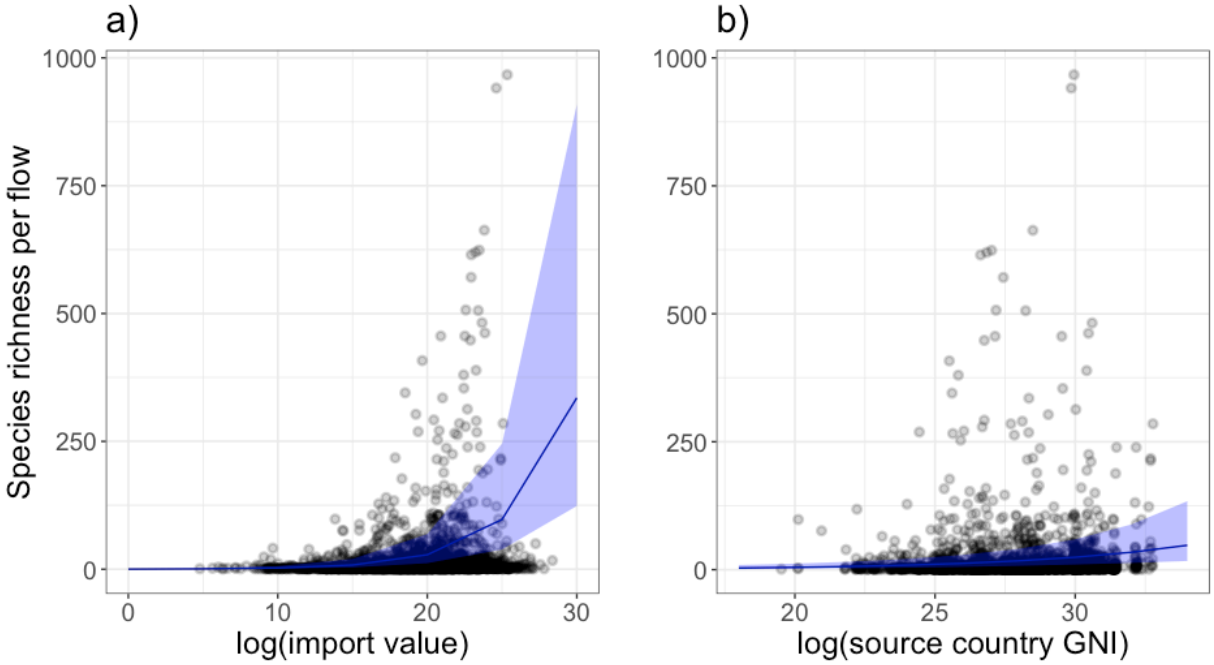

Figure 5. Species richness per flow during transport (estimated by interceptions) as a function of (a) the log transformed import value in US dollars (b) the log transformed Gross National Income (GNI) in the source country in US dollars. The grey circles represent individual flows (unique combinations of source and destination area * commodity class * decade intercepted), and the blue line shows model predictions using the ggpredict() function from the 'ggeffects' package (Lüdecke, 2018). The shaded blue areas represent 95 % confidence intervals.

Whether species were transported within the same biogeographic region or not had a significant effect on the number of species establishing ($\chi^2 = 51.32$, $p < 0.001$) (Figure 4), but not on the number of species being transported ($\chi^2 = 0.12$, $p = 0.734$). Climatic distance did not have a significant impact on transported species richness either ($\chi^2 = 0.05$, $p = 0.822$).

Discussion

We analysed border interception records and lists of established non-native insects to assess the factors driving invasion asymmetry during transport and establishment. Both trade intensity and species' biogeographic origins influenced the size of species flows throughout the invasion process, while the relevance of environmental matching differed pre- and post-introduction.

We found that species from some biogeographic regions were more likely to be transported and establish successfully, but the key donor regions varied between the two stages. During transport, the largest species flows generally arrived from the Nearctic, Panamaian and Neotropical regions. Yet flows of established species were on average greatest for flows originating from the Western Palearctic, Neotropical, and Australasian and Oceanian regions. Similarly, Isitt *et al.* (2023) found that Europe (i.e., the Western Palearctic) was the dominant source of established non-native insects between North America, Europe, and Australasia. It is possible that the difference in dominant donor regions between stages is due to the specific data we analysed, but it may also be that species which are particularly successful at entering introduction pathways, and at successfully establishing once introduced arrive from different regions. We currently lack sufficient information to explore this further, but it would be an interesting focus for future studies on insect introductions. Due to the limited number of areas with data available for both invasion stages, the ranking of donor regions we observed may not be the same for insect exchanges globally. Furthermore, important introduction pathways such as mail and airline baggage may not be sufficiently captured by our model variables, and would require further study using representative data. The observed asymmetry in flows during transport may also be biased by the varying breadth and focus of inspections between destination countries, alongside differences in import volume, production practices, trade partners, and biosecurity measures (Saccaggi *et al.*, 2016; Turner *et al.*, 2021). Inspections often focus on introduction pathways that are considered particularly high-risk, and targeted inspections could thus generate more species detections with goods from certain regions (Eschen, Roques and Santini, 2015). We have also only considered records identified to species level, which may not be representative of less easily identifiable taxa. Randomized, statistically sound inspection systems, such as the USDA Agricultural Quarantine Inspection Monitoring system (USDA, 2011), would provide greater power to assess pathway risks and understand patterns in insect introductions.

We found that species richness increased significantly with import value during both stages, and that more species were transported from countries with a higher GNI. This likely reflects the dominant effect of trade on propagule- and colonization pressure (Levine and D'Antonio, 2003). The socio-economic and development status of a country likely influences their environmental standards and capacity to implement biosecurity measures (Brenton-Rule, Barbieri and Lester, 2016). While the effect of broad socio-economic variables like GDP or GNI on establishment success is debated (Westphal *et al.*, 2008; Sharma, Esler and Blignaut, 2010; Brenton-Rule, Barbieri and Lester, 2016), more precise measures, such as the value of relevant commodity imports, appear to be better predictors of invasion risk for unintentionally introduced taxa (Ollier and Bertelsmeier, 2022). Isitt *et al.* (2023) conclude that plant introductions driven by European colonization is the most compelling explanation for the invasion asymmetry they observed, while native species pool sizes and total import values have little effect. The contrasting influence of trade value in our study may be due to using import values for plant products, a key insect introduction pathway (Kiritani and Yamamura, 2003; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019; Fenn-Moltu *et al.*, 2022), rather than total import values to predict establishments and trade value per commodity type at the transport stage. As well as increasing opportunities for introduction, greater trade intensity could improve the chances of species establishing through repeated introductions (Lockwood, Cassey and Blackburn, 2005). Isitt *et al.* (2023) further found no evidence for the hypothesis that a larger pool of native species leads to proportionally more species being exported. However, the history of European colonization in North America, and Australia and New Zealand may have obscured the impact of native species pool size.

We did not detect a significant effect of relevant treaties, regulations and legislation on non-native species richness at either stage, suggesting that regulatory efforts have a limited impact on insect introductions. This is in contrast with previous work, where a wider set of development and governance indicators indicated a greater risk of non-native species arriving from "poorly regulated" countries (Brenton-Rule, Barbieri and Lester, 2016). The regulatory efforts we considered were not specific to insect invasions however, and it is possible that analysing more targeted regulations would be a better predictor of insect species movements. Turbelin, Malamud and Francis (2017) state that while much of regulation is focused on introductions, control, and management of current invasive species, fewer measures are in place to prevent species being exported. They suggest that while countries are often concerned with non-native species within their borders, less attention is given to preventing species from leaving unless there are known public health impacts. Additionally, there is geographical bias in the information available on regulatory efforts, representing either a lack of data or a genuine lack of policy (Turbelin, Malamud and Francis, 2017). If the latter applies, developing biosecurity efforts in these areas could help limit new introductions and reduce the spread and impact of existing non-native species (Early *et al.*, 2016; Sikes *et al.*, 2018).

While biogeography and trade intensity were important for insect flows throughout the invasion process, the influence of environmental matching (exchanges within or between regions, climatic distance) differed pre- and post-introduction. We found that more species were able to establish when introduced within their native biogeographic region, but, along with climatic distance, this did not influence species flows during transport. The impact of environmental similarity on establishment success has been shown in previous studies, for example in fruit flies (Trombik *et al.*, 2022), reptiles and amphibians (Bomford *et al.*, 2009; Capinha *et al.*, 2017), and mammals (Broennimann *et al.*, 2021). Similarly, for insects, analogous climates have been used to identify potential sources of non-native species (Peacock and Worner, 2006; Worner and Gevrey, 2006), and insect invasions have further been linked to climate change (Ward and Masters, 2007; Renault *et al.*, 2018). Environmental similarity after introduction could potentially affect spread rates as well as establishment success (Abellán *et al.*, 2017). Furthermore, we found that the number of transported species decreased with geographic distance, similarly to Suhr et al (2019). This could potentially be due to lower survival rates over longer journeys, but we would need additional information on survival and detectability to verify this.

Our results support previous research highlighting globalization as a key driver of invasion patterns, and reinforces the importance of including processes occurring prior to establishment in analyses of invasion risk (Hulme, 2009; Chapman *et al.*, 2017; Essl *et al.*, 2020; Bonnamour, Gippet and Bertelsmeier, 2021). Using border interceptions to quantify flows of insects during transport allows us to assess the factors influencing this largely unobserved stage of the invasion process. Moving forward, thorough records of introductions, establishments, and native species from a wider range of areas, including developing countries, would provide a more comprehensive picture of the invasion risk presented by trade between different biogeographic regions. More precise information on the native ranges of established species could further improve our understanding of the link between climatic conditions and establishment success. Ultimately, biosecurity resources are limited both nationally and internationally, and any information that enables more efficiently targeted measures is of considerable value for limiting insect invasions.

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Data accessibility statement: The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.dv41ns243.

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Supplementary material: chapter 2

Table S1. The interception records identified to species level and with information on the associated commodity available for each of the seven destination areas.

Destination	Data collection	Years covered	Interception events	Species (+ additional genera)	Commodity classes	Source countries
Canada	Canadian Food Inspection Agency	1997-2019	2964	893	9	88
Japan	Ministry of Agriculture, Forestry and Fisheries	1997-2017	32125	1398	4	129
New Zealand	Scion BUGS database, New Zealand Ministry for Primary Industries (or predecessors recorded under different names)	1960-2013 Formicidae 1960-2000 Forest insects	10191	514	14	121
Mainland United States of America	US Department of Agriculture, Animal & Plant Health Inspection Service, Department of Homeland Security, Customs and Border Protection	1998-2018 1960-2019 Formicidae 1960-1982 Thysanoptera 1960-2000 Forest insects	1484999	6765	14	219
Hawaii	US Department of Agriculture, Animal & Plant Health Inspection Service, Department of Homeland Security, Customs and Border Protection	1998-2018	17359	446	10	47
South Africa	South African Department of Agriculture, Land Reform and Rural Development. Available from Saccaggi et al. 2021, https://doi.org/10.6084/m9.figshare.c.5180681.v1	1995-2019	2319	305	2	65

Table S2. The commoditiy classes insects were intercepted with. The HS-2 commodity codes included in each class refer to chapters in the international Harmonized Commodity Description and Coding Systems (World Customs Organization, 2021).

Commodity class	**HS-2 code and full description**
Animal products	01 Animals; live, 02 Meat and edible meat offal, 03 Fish and crustaceans, molluscs and other aquatic invertebrates, 04 Dairy produce; birds' eggs; natural honey; edible products of animal origin, not elsewhere specified or included, 05 Animal originated products; not elsewhere specified or included, 41 Raw hides and skins (other than furskins) and leather, 42 Articles of leather; saddlery and harness; travel goods, handbags and similar containers; articles of animal gut (other than silk-worm gut)
Plant products	06 Trees and other plants, live; bulbs, roots and the like; cut flowers and ornamental foliage, 07 Vegetables and certain roots and tubers; edible, 08 Fruit and nuts, edible; peel of citrus fruit or melons, 09 Coffee, tea, mate and spices, 10 Cereals, 11 Products of the milling industry; malt, starches, inulin, wheat gluten, 12 Oil seeds and oleaginous fruits; miscellaneous grains, seeds and fruit, industrial or medicinal plants; straw and fodder, 13 Lac; gums, resins and other vegetable saps and extracts, 14 Vegetable plaiting materials; vegetable products not elsewhere specified or included, (1111) soil around plants, 53 Vegetable textile fibres; paper yarn and woven fabrics of paper yarn
Foodstuffs	15 Animal or vegetable fats and oils and their cleavage products; prepared animal fats; animal or vegetable waxes, 16 Meat, fish or crustaceans, molluscs or other aquatic invertebrates; preparations thereof, 17 Sugars and sugar confectionery, 18 Cocoa and cocoa preparations, 19 Preparations of cereals, flour, starch or milk; pastrycooks' products, 20 Preparations of vegetables, fruit, nuts or other parts of plants, 21 Miscellaneous edible preparations, 22 Beverages, spirits and vinegar, 23 Food industries, residues and wastes thereof; prepared animal fodder, 24 Tobacco and manufactured tobacco substitutes
Mineral products	25 Salt; Sulphur; earths, stone; plastering materials, lime and cement, 26 Ores, slag and ash, 27 Mineral fuels, mineral oils and products of their distillation; bituminous substances; mineral waxes
Chemical products	28 Inorganic chemicals; organic and inorganic compounds of precious metals; of rare earth metals, of radio-active elements and of isotopes, 29 Organic chemicals, 30 Pharmaceutical products, 31 Fertilizers, 32 Tanning or dyeing extracts; tannins and their derivatives; dyes, pigments and other colouring matter; paints, varnishes; putty, other mastics; inks, 33 Essential oils and resinoids; perfumery, cosmetic or toilet preparations, 34 Soap, organic surface-active agents; washing, lubricating, polishing or scouring preparations; artificial or prepared waxes, candles and similar articles, modelling pastes, dental waxes and dental preparations with a basis of plaster, 36 Explosives; pyrotechnic products; matches; pyrophoric alloys; certain combustible preparations
Plastics/Rubber	39 Plastics and articles thereof, 40 Rubber and articles thereof
Wood products	44 Wood and articles of wood; wood charcoal, 45 Cork and articles of cork, 46 Manufactures of straw, esparto or other plaiting materials; basketware and wickerwork, 47 Pulp of wood or other fibrous cellulosic material; recovered (waste and scrap) paper or paperboard, 48 Paper and paperboard; articles of paper pulp, of paper or paperboard, 49 Printed books, newspapers, pictures and other products of the printing industry; manuscripts, typescripts and plans

Textiles	50 Silk, 51 Wool, fine or coarse animal hair; horsehair yarn and woven fabric, 52 Cotton, 54 Man-made filaments; strip and the like of man-made textile materials, 56 Wadding, felt and nonwovens, special yarns; twine, cordage, ropes and cables and articles thereof, 57 Carpets and other textile floor coverings, 61 Apparel and clothing accessories; knitted or crocheted, 62 Apparel and clothing accessories; not knitted or crocheted, 63 Textiles, made up articles; sets; worn clothing and worn textile articles; rags
Footwear/Headgear	64 Footwear; gaiters and the like; parts of such articles, 66 Umbrellas, sun umbrellas, walking-sticks, seat sticks, whips, riding crops; and parts thereof
Stone/Glass	68 Stone, plaster, cement, asbestos, mica or similar materials; articles thereof, 69 Ceramic products, 70 Glass and glassware
Metal products	72 Iron and steel, 73 Iron or steel articles, 74 Copper and articles thereof, 75 Nickel and articles thereof, 76 Aluminium and articles thereof, 80 Tin; articles thereof, 81 Metals; n.e.c., cermets and articles thereof, 82 Tools, implements, cutlery, spoons and forks, of base metal; parts thereof, of base metal, 83 Metal; miscellaneous products of base metal
Machinery/Electrical	84 Nuclear reactors, boilers, machinery and mechanical appliances; parts thereof, 85 Electrical machinery and equipment and parts thereof; sound recorders and reproducers; television image and sound recorders and reproducers, parts and accessories of such articles
Transport vectors and commodities	86 Railway, tramway locomotives, rolling-stock and parts thereof; railway or tramway track fixtures and fittings and parts thereof; mechanical (including electro-mechanical) traffic signalling equipment of all kinds, 87 Vehicles; other than railway or tramway rolling stock, and parts and accessories thereof, 88 Aircraft, spacecraft and parts thereof, 89 Ships, boats and floating structures
Miscellaneous	67 Feathers and down, prepared; and articles made of feather or of down; artificial flowers; articles of human hair, 90 Optical, photographic, cinematographic, measuring, checking, medical or surgical instruments and apparatus; parts and accessories, 91 Clocks and watches and parts thereof, 92 Musical instruments; parts and accessories of such articles, 93 Arms and ammunition; parts and accessories thereof, 94 Furniture; bedding, mattresses, mattress supports, cushions and similar stuffed furnishings; lamps and lighting fittings, n.e.c.; illuminated signs, illuminated name-plates and the like; prefabricated buildings, 95 Toys, games and sports requisites; parts and accessories thereof, 96 Miscellaneous manufactured articles, 97 Works of art; collectors' pieces and antiques

Table S3. Insect species richness from each biogeographic region listed as established in our dataset, and the estimated pool of native insect species present in that region. The Eastern and Western Palearctic, and the Sino-Japanese and Oriental regions are aggregated here as we lack estimates of the native species pool for each separately.

Biogeographic region	Number of species from the region established in our destinations*	Estimated pool of native insects**
Eastern + Western Palearctic	1780 (2057)	648 040
Neotropical	561 (613)	162 0348
Australasian	512 (609)	720 521
Nearctic	394 (468)	147 329
Sino-Japanese + Oriental	365 (418)	734 822
Oceanian	263 (274)	240 720
Afrotropical	119 (169)	975 179

Panamaian	4 (8)	614 918
Madagascan	0 (0)	-
Saharo-Arabian	0 (1)	-

*The number in parentheses includes the widespread species that have established in our destination areas but were excluded from the analyses.

** Estimates from Stork (2018). The estimate for the Nearctic is from (Danks and Smith, 2017).

Figure S1. Biogeographic regions of the world based on Holt *et al*. (2013), with the Palearctic divided into the Eastern and Western Palearctic. The broad-scale realms delineated by Holt *et al*. (2013) are based on the distributions and phylogenetic turnover of amphibian, bird, and mammal species.

Table S4. The output of the model predicting species richness per flow during transport (measured using interceptions).

Variable	**X^2**	**Direction of effect**	**p-value**
Import value	136.91	↑	< 0.001 ***
Commodity class	2398.46	-	< 0.001 ***
Biogeographic region	29.26	-	0.001 **
Source species pool	3.31	↑	0.069 .
Regulations per source country	0.01	↑	0.926

Regulations per destination country	1.94	↓	0.163
Gross National Income (GNI)	19.52	↑	< 0.001 ***
Climatic dissimilarity	0.05	↑	0.830
Geographic distance	10.31	↓	0.001
Within regions (compared to between)	0.01	↓	0.933
Import value * Commodity class	79.93	-	< 0.001 ***

Table S5. The output of the model predicting established species richness per flow.

Variable	X^2	Direction of effect	p-value
Import value of plant products	246.26	↑	< 0.001 ***
Biogeographic region	410.10	-	< 0.001 ***
Within regions (compared to between)	51.32	↑	< 0.001 ***
Regulations per destination	0.22	↓	0.643

Chapter 3: Pathways for accidental biocontrol: the human-mediated dispersal of insect predators and parasitoids

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Abstract

Introductions of insect predators and parasitoids for biological control is a key method for pest management. Yet in recent decades, biological control has become more strictly regulated and less frequent. Conversely, the rate of unintentional insect introductions through human activities is rising. While accidental introductions of insect natural enemies can potentially have serious ecological consequences, they are challenging to quantify as their movements go largely unobserved. We used historical border interception records collected by the US Department of Agriculture from 1913 to 2018 to describe the diversity of entomophagous insects transported unintentionally, their main introduction pathways, and trends in host specificity. There were 35,312 interceptions of insect predators and parasitoids during this period, representing 93 families from 11 orders, and 196 species from these families. Commodity associations varied, but imported plants and plant products were the main introduction pathway. Most interceptions originated with commodities imported from the Neotropical, Panamaian and Western Palearctic regions. Among the intercepted species, 27 % were found in material originating from more than one country. Two thirds of species were polyphagous host generalists. Furthermore, 25 % of species had already been introduced intentionally as biological control agents internationally, and 4.6 % have documented negative impacts on native biodiversity or human society. Most of the intercepted species that have not established in the USA are host generalists or have at least one known host species available. The unintentional transport of diverse natural enemy insects has potential to cause substantial ecological impacts, both in terms of controlling pests through accidental biocontrol and disrupting native communities. Characterising the insects being transported and their introduction pathways can inform biosecurity practices and management.

Keywords: *Accidental biocontrol, border interceptions, insects, introduction pathways, parasitoids, predators, Human-mediated dispersal*

Introduction

Insects are among the most common and damaging animal invaders in terrestrial ecosystems, costing at least 70 billion US $ annually (Bradshaw *et al.*, 2016). Insects are also extremely diverse, and occupy almost every terrestrial habitat, so it is perhaps unsurprising that they have become such successful invaders. Unlike many non-native plants and vertebrates, insects are generally introduced unintentionally through human activities, either as contaminants of commodities that are part of their natural habitat, or as hitchhikers associated with other transported commodities (Gippet *et al.*, 2019). While most non-native insects go relatively unnoticed, a subset generate negative ecological or economic impacts in their new range (Hill *et al.*, 2016).

We use ‘non-native’ to refer to species introduced outside of their native range by humans, either intentionally or accidentally, and ‘invasive’ to refer to non-native species that are negatively impacting native biodiversity, ecosystem services or human economy and well-being (IUCN, 2000). Many invasive insects are herbivorous plant pests, causing considerable damage to agriculture (Bradshaw *et al.*, 2016; Paini *et al.*, 2016; Tonnang *et al.*, 2022) and forestry (Holmes *et al.*, 2009; Aukema *et al.*, 2011). These invasive herbivores are economically important (Pimentel, 2005), and are the primary focus of most biosecurity measures. Nevertheless, introductions of entomophagous insects are also of considerable importance for both native and non-native biodiversity (Louda *et al.*, 2003; Snyder and Evans, 2006; Kenis *et al.*, 2009).

While most insect introductions are unintentional, releases of entomophagous insects have become integral to pest management around the world (Hajek and Eilenberg, 2018). Importation (or classical) biological control involves introducing species’ natural enemies, commonly parasitoids or sometimes predators against invertebrate pests, to suppress populations in their non-native range (Heimpel and Mills, 2017). In total, there have been more than 6000 intentional insect introductions for biological control worldwide (Cock *et al.*, 2016). However, after Howarth (1983) criticising the inherent risks, there have been significant concerns raised about non-target and indirect effects (e.g., Simberloff and Stiling, 1996; Ewel *et al.*, 1999). Consequently, stricter regulations have been implemented in many countries, requiring that potential biological control agents are carefully tested to determine their host specificity, efficacy, and climatic suitability (FAO, 2005; Hajek *et al.*, 2016).

Fewer intentional introductions have been carried out in recent years (Cock *et al.*, 2016; Hajek *et al.*, 2016), but the rate of unintentional introductions continues to rise (Seebens *et al.*, 2017). This includes entomophagous insects, which may provide opportunities for pest control but could also have profound direct and indirect effects on native biodiversity. Non-native predatory insects, particularly those with generalist feeding habits, may displace native species and cause widespread impacts on the communities they invade (reviewed in Snyder and Evans, 2006). For example, the European wasps *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae) both prey on and outcompete native species in New Zealand and Australia (Beggs, 2001; Kasper *et al.*, 2004). Accidentally introduced parasitoids may also have significant ecological impacts, for example, *Echthromorpha intricatoria* (Hymenoptera: Ichneumonidae) is likely involved in the decline of native butterfly *Bassaris gonerilla* (Lepidoptera: Nymphalidae) in New Zealand (Barron, Wratten and Barlow, 2004). Conversely, there are also unintentional introductions that would be judged successful if they had been carried out intentionally, such as *Macroglenes penetrans* (Hymenoptera: Pirenidae) parasitising the wheat midge, *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) in North America (Thompson and Reddy, 2016).

All introduced species must overcome a series of biotic and abiotic barriers to establish and spread (Blackburn *et al.*, 2011; Schulz, Lucardi and Marsico, 2021). Nevertheless, as biological control agents are carefully chosen before their transport and release, the selection pressures they face prior to establishment differ from unintentional introductions (Müller-Schärer and Schaffner, 2008). The host-specificity testing in place for biological control agents aims to select specialist species that effectively suppress their target host without impacting populations of other species. Conversely, the processes leading to accidental biocontrol may select for widespread, generalist species that are more likely to become associated with human-mediated dispersal pathways (Gippet *et al.*, 2019), and to find alternative hosts or prey wherever they are introduced (Chapple, Simmonds and Wong, 2012). Additionally, traits that are advantageous for biological control, such as parthenogenesis, good dispersal ability, and rapid population growth, may also increase the probability of non-target effects when there are native species within the potential host range (Louda *et al.*, 2003).

Managing biological invasions becomes increasingly difficult as invading populations spread and grow (Leung *et al.*, 2002; Venette *et al.*, 2021). Knowledge of introduction pathways is therefore crucial for implementing effective prevention methods early on, including trade regulations, interception programmes, screening systems and early warning strategies (Hulme, 2006). In this paper we describe the unintentional transport of insect predators and parasitoids to the USA over more than a century (1913-2018). Using border interception records, we explore 1) which natural enemy (entomophagous) taxa are transported unintentionally, 2) which world regions they are arriving from, and 3) what their main introduction pathways are. For the records identified to species-level, we further explore 4) the host specificity of transported predators and parasitoids, and 5) their invasion history and the presence of known hosts.

Methods

Curation of border interceptions

We analysed border interception records collected by US Department of Agriculture and US Department of Homeland Security inspectors between 1913 and 2018. These records were based on insects detected during inspections of international cargo, mail, vessels, and passenger baggage arriving at ports-of-entry (McCullough *et al.*, 2006)**.** While border interceptions do not directly represent introductions, they can be considered a proxy for species' undetected arrival (Turner *et al.*, 2021)**.** Nevertheless, commodities or pathways that are considered particularly high risk are often inspected preferentially, and organisms vary in their probability to be detected and recorded during inspections (Mally *et al.*, 2022)**.** We grouped exporting countries into biogeographic regions as per Holt *et al.* (2013), with the large Palearctic region divided into the Eastern and Western Palearctic (Figure S1). Commodities were classified according to the Harmonized Commodity Description and Coding System (HS) (World Customs Organization, 2021), and chapters (HS-2) grouped into broad classes based on the type of product (Table S2). Further details on data sources and cleaning are available in the supplementary material.

Selecting parasitoid and predator families

As a considerable proportion of interceptions are not identified to species- or genus-level, we targeted families where all or most species are predators or parasitoids of other invertebrates. We listed families of parasitoid Hymenoptera based on Weber *et al.* (2021) and added additional families known to primarily include parasitoids. We listed primarily predatory families based on Liebhold *et al.* (2021), and added families from Hörren *et al.* (2022) which we verified as being largely predators based on internet searches. This resulted in a target list of 194 families belonging to 15 orders (Table S1). Entomophagous species from other families were not included in this study. We further compared families intercepted from 1913-2018 with families intercepted from 2000-2018, the period following the passage of the USA Plant Protection Act which regulated 'any enemy, antagonist or competitor used to control a plant pest or noxious weed' (Hunt *et al.*, 2008).

Host specificity and invasion status

Host specificity refers to the level of specificity of a parasitoid or predator to its host or prey (Frank and Gillett-Kaufman, 2006). We classified species as monophagous (hosts or prey from one genus), stenophagous (hosts or prey from one super-family), oligophagous (hosts or prey from one order), or polyphagous (hosts or prey from multiple orders). Detailed methods are available in the supplementary material. We excluded from our analyses species within our target families that are known not to be parasitoids or predators.

We further defined species as 'transported species': all those intercepted during border inspections, 'established species': non-native species that have established a self-sustaining population in their non-native range, 'invasive species': established non-native species that have documented negative impacts on native biodiversity or human well-being, 'biocontrol agents': species intentionally introduced for biological control or that have been studied as potential biological control agents, or 'invasive biocontrol agents': species intentionally introduced as biological control agents that have documented negative impacts on native biodiversity or human wellbeing. Detailed methods are available as supplementary material. All analyses were carried out in R (R Core Team, 2023).

Commodity associations

To explore the relationship between insect families and the commodities they were transported with, we calculated the proportion of interceptions on each HS-2 commodity group for the 46 families intercepted at least 20 times. We plotted this relationship using the pheatmap() function from the 'pheatmap' package (Kolde, 2019). We then carried out a Correspondence Analysis using the 'ade4' package (Dray and Dufour, 2007). To quantify the degree of specialization in commodity associations, we considered interactions between insects and commodities as a bipartite network. We calculated the d' index of specialization from the 'bipartite' package

(Dormann, Gruber and Fründ, 2008) for families intercepted at least 20 times, and for species intercepted at least ten times. The d' statistic is based on discrimination from a random selection of interaction partners, in this case commodities that insects were transported with, ranging from the most generalized (0) to the most specialized (1) (Blüthgen, Menzel and Blüthgen, 2006). We compared the degree of specialization in commodity associations between parasitoid families, predator families and other insect families intercepted at least 20 times using a Kruskal-Wallis test from the 'stats' package (R Core Team, 2023). We then performed pairwise comparisons between groups using the dunnTest() function from the 'FSA' package with p-values adjusted for multiple comparisons using the Holm method (Ogle *et al.*, 2023). We further compared commodity specialization between monophagous, stenophagous, oligophagous, and polyphagous species, as well as between species that have established in the USA vs. those that have not established, using a Kruskal-Wallis test as above.

Results

There were 35,312 interceptions of insect predators and parasitoids between 1913 and 2018. Of these, 4.0 % were identified to the species-level and 93 different families were detected, belonging to eleven orders (Figure 1). All of these, except Euphaeidae (Odonata) and Asopinae (Hemiptera: Pentatomidae), were intercepted after 2000. The orders with the most interceptions of predators and parasitoids were Coleoptera (45.0 % of interceptions), Hemiptera (32.7 %), Hymenoptera (19.7 %) and Diptera (1.9 %) (Figure 1a). The Neuroptera, Mantodea, Odonata, Raphidioptera, Strepsiptera (endoparasites), Dermaptera and Trichoptera together made up less than 1 % of interceptions.

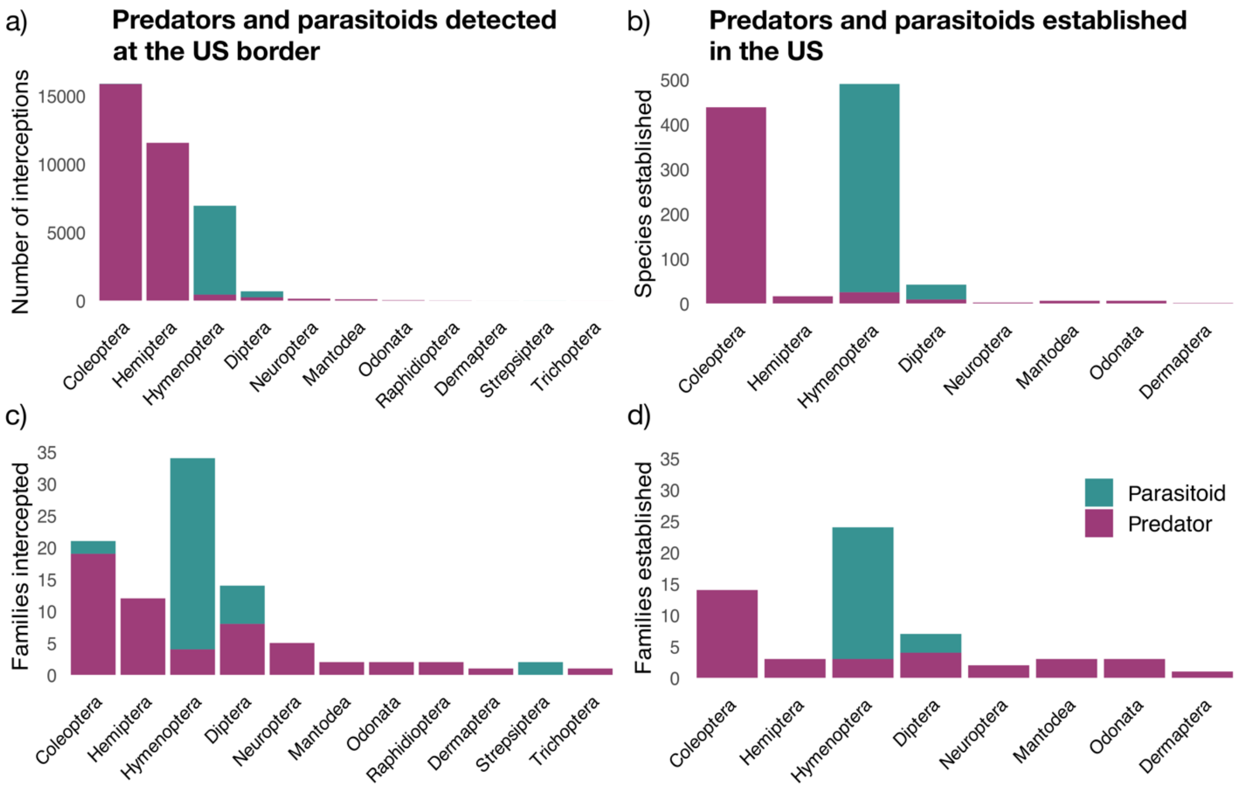

Figure 1. Non-native insect parasitoids (pink) and predators (turquoise) by order. a) The number of interception events, b) the number of established species, c) the number of families intercepted, and d) the number of established families.

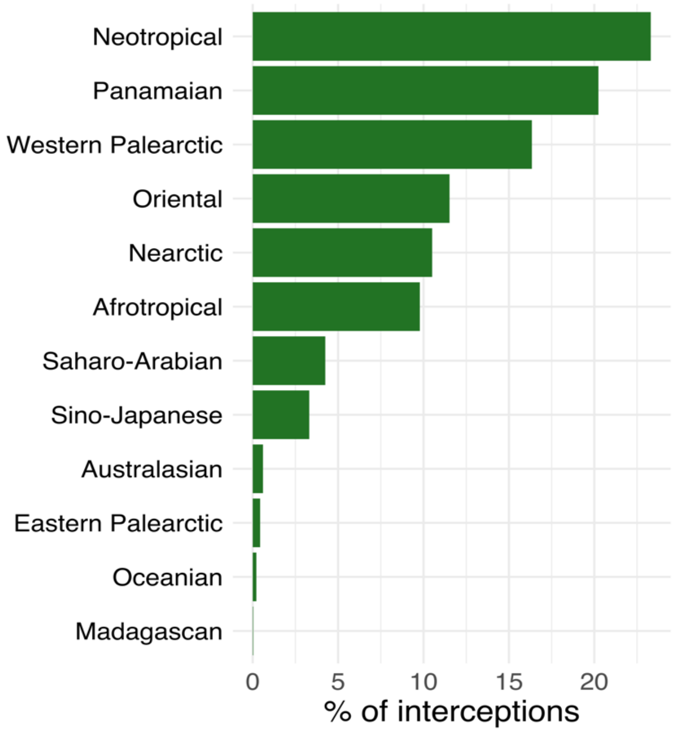

Figure 2. The biogeographic regions where commodities transporting insect predators and parasitoids to the USA were imported from.

Hymenoptera (34 families), Coleoptera (21), Diptera (14) and Hemiptera (12) had the greatest numbers of families intercepted (Figure 1c). Conversely, relatively few predatory or parasitoid Hemiptera and Hymenoptera have established in the USA (Figure 1b, 1d). Within the families we analysed, there were 157 predator and 39 parasitoid species identified. The parasitoid species were almost all Hymenoptera (35 species from 13 families), plus the beetle *Aulonosoma tenebrioides* (Passandridae), and three Tachinidae species (*Ectophasia crassipennis, Lixophaga sphenophori* and *Voria ruralis*). The predators were mostly Coleoptera (79 species), Hemiptera (45) and Hymenoptera (24), along with two Diptera, two Mantodea, one Neuroptera and one Dermaptera species. Most natural enemy interceptions in the USA arrived with commodities imported from the Neotropical (23.1 %), Panamaian (20.0 %) and Western Palearctic regions (16.4 %) (Figure 2). Of the 196 species detected, 53 were recorded arriving from more than one country, and 43 from more than one region.

Natural enemies were discovered with 14 different commodity classes during inspections (Table S2). While there was variation in commodity associations between families (Figure 3), both the most interceptions, and the greatest number of insect families arrived with commodities classified as ‘plants and plant products’ (Figure 4a). There was a high proportion of interceptions with ‘stone/glass products’ for insects arriving from the Western Palearctic, largely ceramic tiles (Figure 4a). The specific type of ‘plants and plant products’ transporting insects also differed depending on their origin (Figure 4b). Overall, the HS-2 commodities most frequently associated with natural enemies were ‘live plants and cut flowers’, ‘coffee, tea, herbs, and spices’, ‘fruit and nuts’, ‘vegetables’, ‘ceramics’, and ‘cereals’.

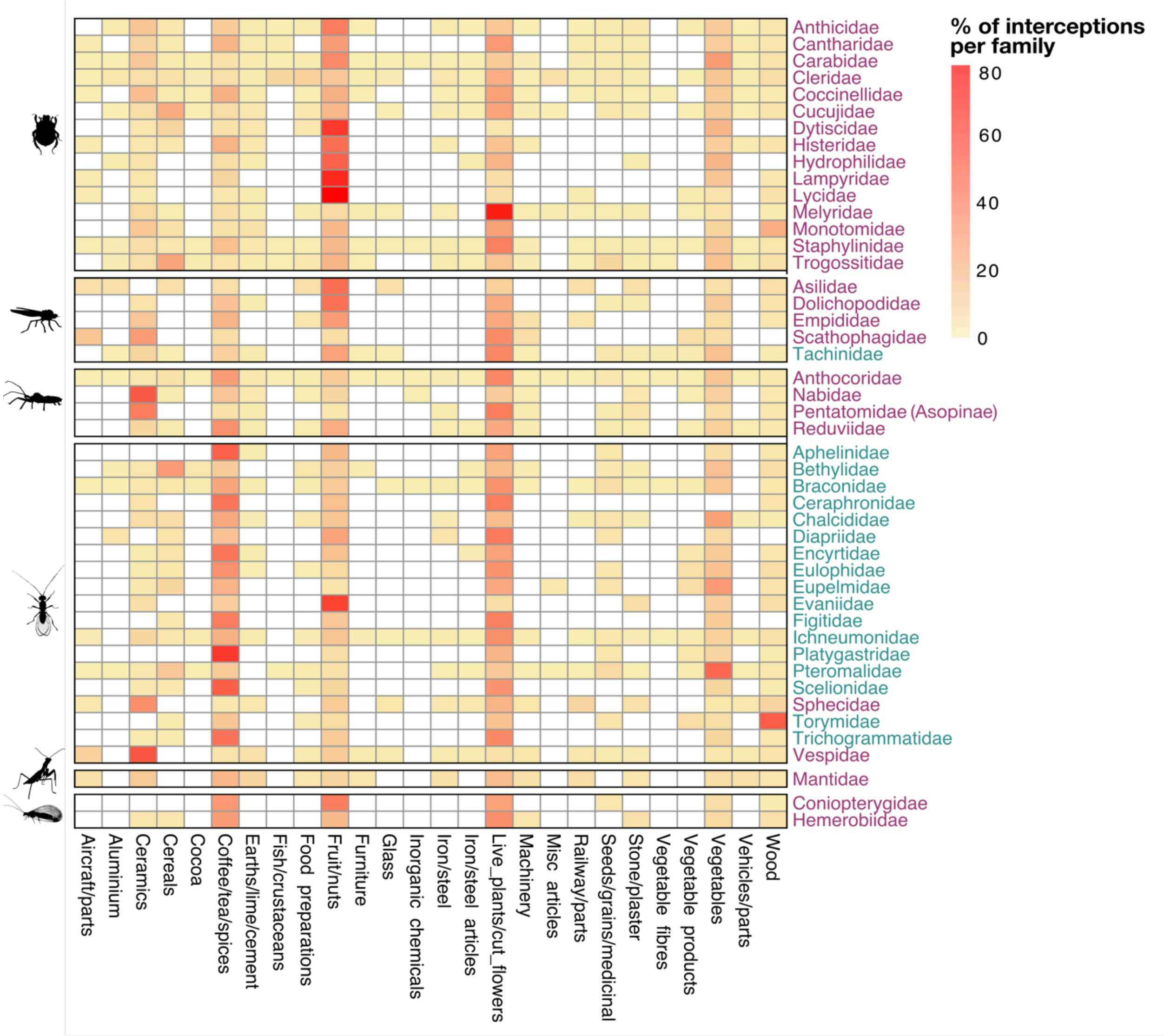

Figure 3. Commodity associations of predator (pink) and parasitoid families (turquoise). Only families and HS-2 commodity groups with at least 20 interceptions are plotted. Families are grouped by order: Coleoptera, Diptera, Hemiptera, Hymenoptera, Mantodea, and Neuroptera from top to bottom. The heatmap is coloured by the percentage of interceptions per family on each commodity.

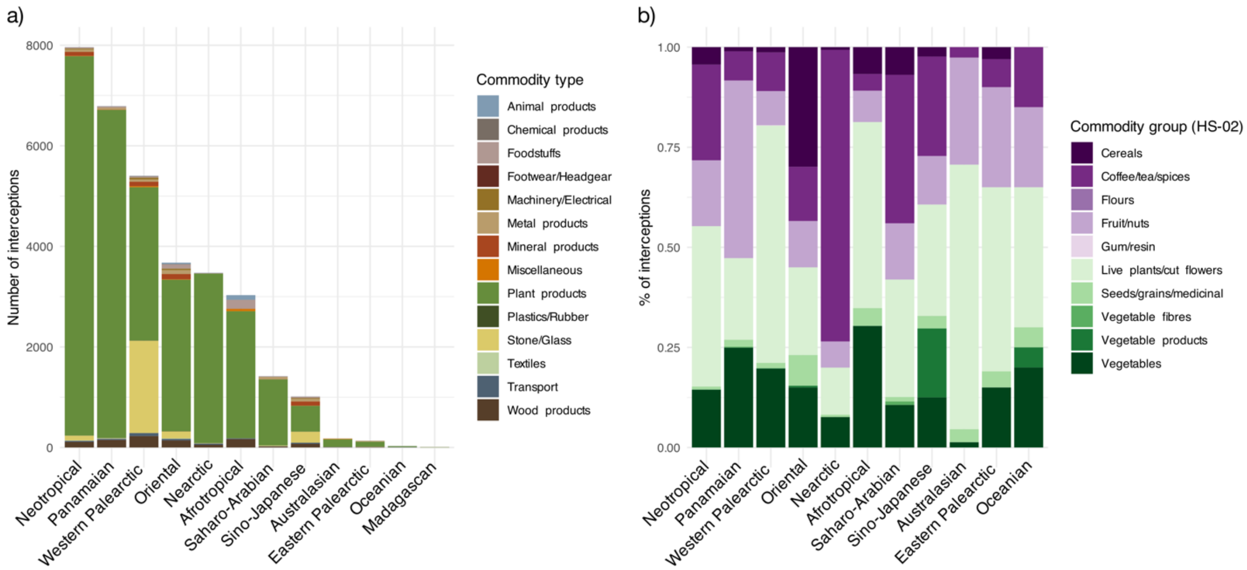

Figure 4. Biogeographic region of origin for commodities transporting entomophagous insects. a) The number of interceptions per commodity class for each region, and b) the percentage of interceptions with commodities classed as ‘plants and plant products’ per region.

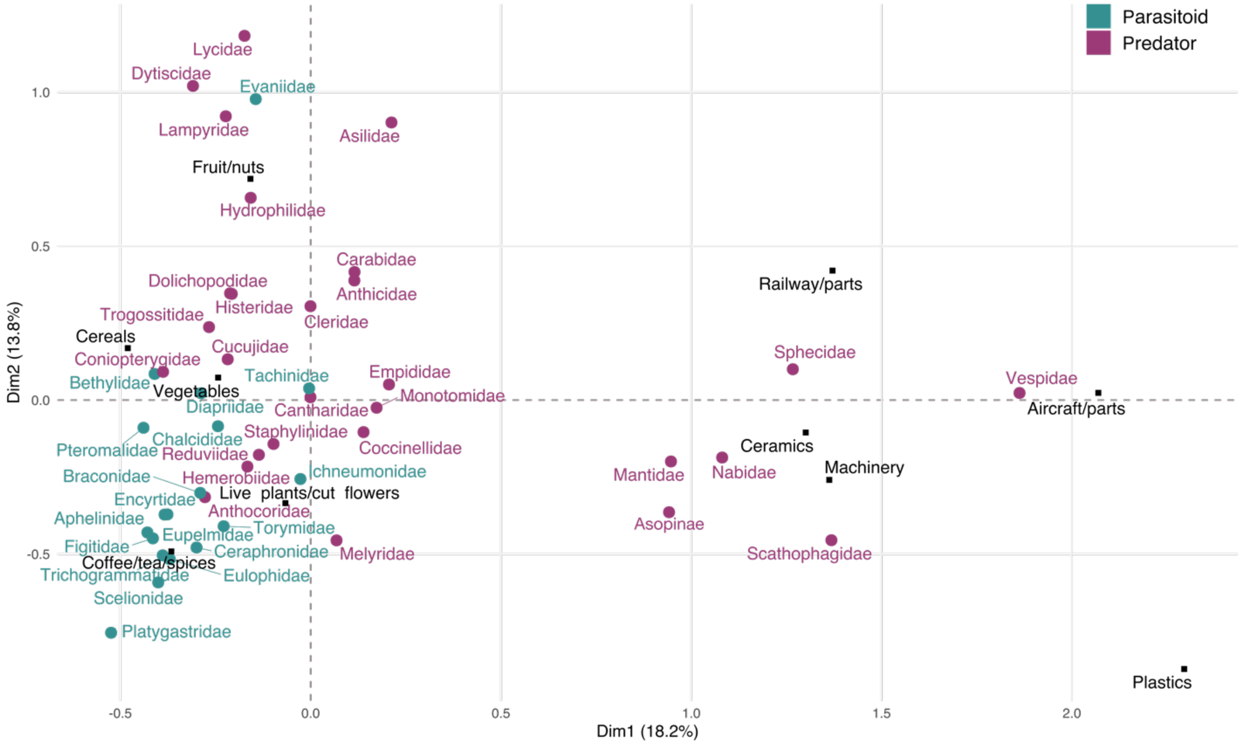

Figure 5. Correspondence analysis of commodity associations by family. Predators are pink, parasitoids turquoise. The ten HS-2 commodities contributing the most to the ordination are labelled in black.

Predatory Vespidae, Scathophagidae, Sphecidae, Nabidae, Asopinae (family Pentatomidae) and Mantidae were mainly associated with inorganic commodities such as ‘ceramics’, ‘machinery’, ‘aircraft/parts’ and ‘railway/parts’, while other predatory families arrived more frequently with ‘fruits and nuts’ and ‘cereals’ (Figure 5). Most parasitoid families were more closely associated with ‘coffee, tea, herbs and spices’, and ‘live plants and cut flowers’. There was a marginally significant difference in commodity specialization between predator families, parasitoid families, and other families of insects being transported (Kruskal-Wallis $\chi^2 = 5.78$, $p = 0.055$) (Figure 6a). Parasitoid families were less specialized in their commodity associations than other families (Dunn’s test, $Z = 2.39$, $p = 0.051$). There were 17 species intercepted ten or more times (Figure 6b). Their d' ranged from 0.14 (most generalist, *Harmonia axyridis,* Coleoptera: Coccinellidae) to 0.67 (*Pseuderimerus indicus,* Hymenoptera: Torymidae). Of these 17 species, 12 were polyphagous. There was no significant association between host specificity and commodity specialization (Kruskal-Wallis $\chi^2 = 3.24$, $p = 0.35$), nor between commodity specialization and whether the species have established in the USA or not (Kruskal-Wallis $\chi^2 = 0.01$, $p = 0.92$). However, the four parasitoid species intercepted ten or more times were significantly more specialized in their commodity associations than the predator species (Kruskal-Wallis $\chi^2 = 3.71$, $p = 0.05$) (Figure S2).

Of all natural enemy species detected at the border, 66.8 % were polyphagous host generalists, 15.8 % were oligophagous generalists, and 13.8 % stenophagous specialists (Figure 7). Just three species were classed as monophagous, the parasitoids *Pseuderimerus indicus* (Hymenoptera: Torymidae)*, Lixophaga sphenophori* (Diptera: Tachinidae) and *Hexacola neoscatellae* (Hymenoptera: Figitidae), although this could be due to limited information on their hosts. The pattern was similar for records after 2000 when the most interceptions occurred, and more strict regulations for intentional introductions of natural enemies were in place.

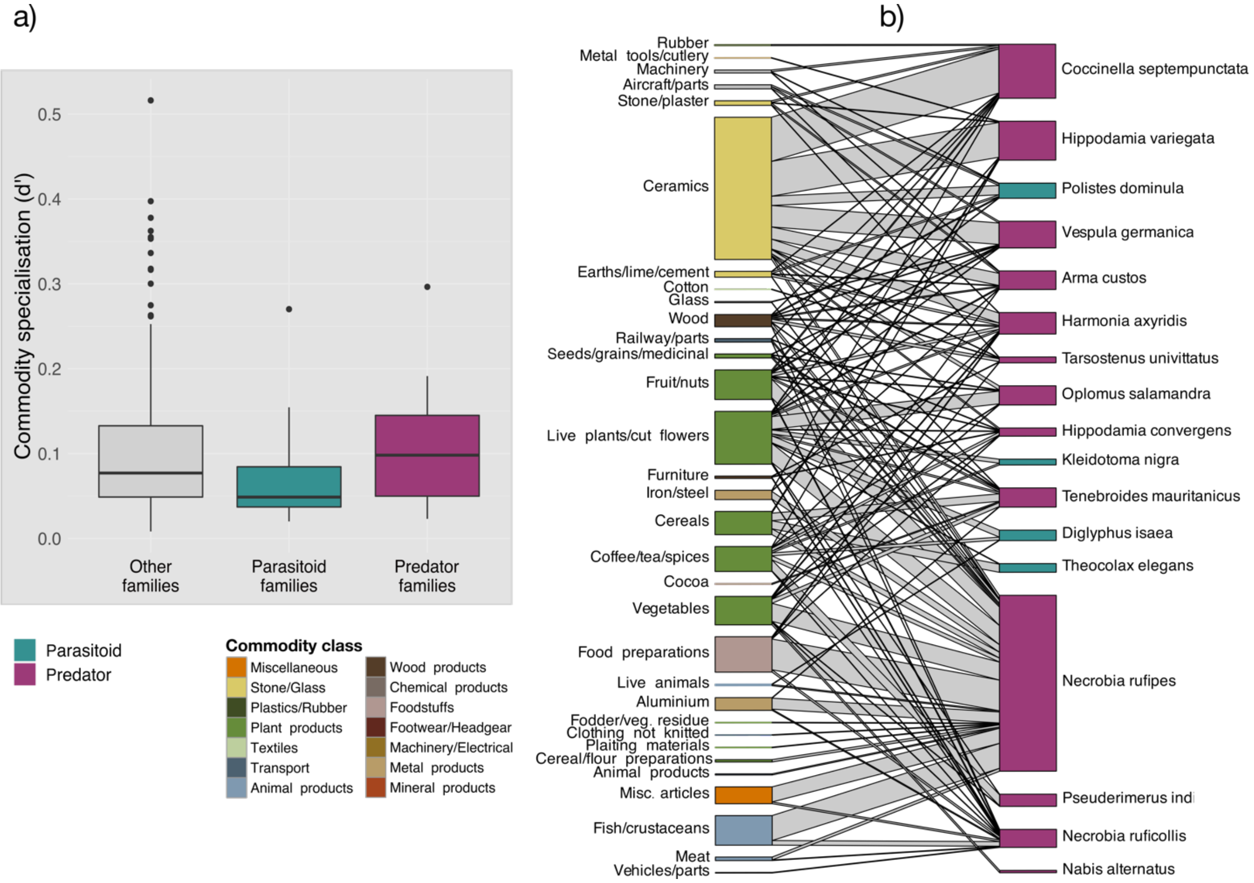

Figure 6: Specialization in commodity associations of parasitoids (turquoise) and predators (pink) during transport. a) Commodity specialization of parasitoid families, predatory families, and other insect families (grey) intercepted 20 or more times. b) Observed interactions between the 17 species intercepted at least ten times and the HS-2 commodity groups they were transported with. Commodities are coloured by the broad product class.

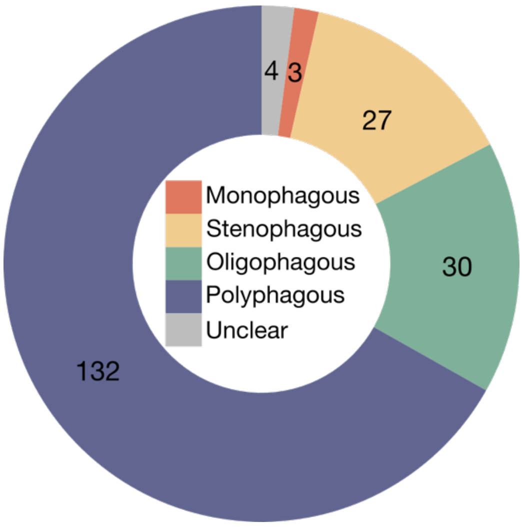

Figure 7. Host specificity of intercepted predator and parasitoid species. Species are monophagous (hosts or prey from one genus), stenophagous (hosts or prey from one super-family), oligophagous (hosts or prey from one order), or polyphagous (hosts or prey from multiple orders).

Several of the intercepted species have already established in the USA (Figure 8a), either through intentional releases, or as unintentional introductions. Other species are considered damaging, i.e., classified as invasive (Simpson *et al.*, 2022). There were nine invasive species intercepted (GRIIS; Pagad *et al.*, 2022), three of which have not established in the USA (Figure 8b, *Ropalidia marginata, Vespula vulgaris* and *Polistes chinensis*, all Vespidae). Of the 196 intercepted species, 50 have been intentionally introduced for biological control either in the USA or elsewhere in the world, and a further 19 species have been studied as potential biological control agents. However, there was no significant association between host specificity and use or consideration for biological control among the species intercepted (Fisher's exact test, p = 0.304). Three of the biological control agents are now considered invasive (*Coccinella septempunctata, Harmonia axyridis* and *Tenodera sinensis*). Of the predator species already established in the USA, 84.3 % were generalists (24 polyphagous, 8 oligophagous). We identified at least one known host species present in the USA for all 11 established parasitoid species, and for 75 % of the parasitoid species that have not (yet) established (21 species). Of the predators that were intercepted but not established, 88.23 % are generalists (90 polyphagous, 15 oligophagous), suggesting that failure to find suitable prey is unlikely to explain their establishment failure.

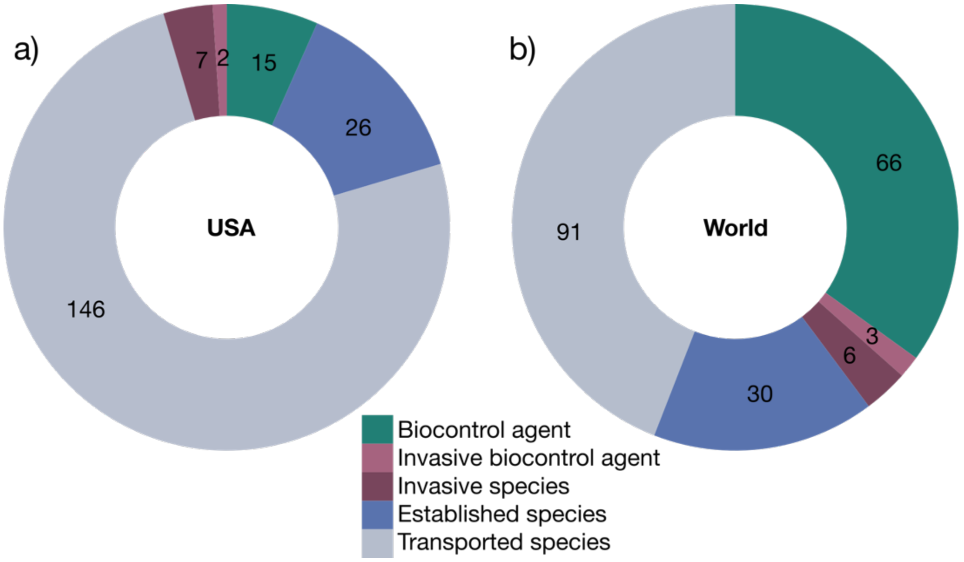

Figure 8. Invasion status of intercepted predator and parasitoid species a) in the USA and b) globally. Transported species (grey) are not otherwise categorised. Biocontrol agents include

both species introduced or studied for biological control. Of 69 world biocontrol species, 47 have successfully established outside their native range.

Discussion

There were 93 families of natural enemy insects from 11 orders recorded at US borders between 1913 and 2018. Most interceptions originated from within the Americas (Neotropical and Panamaian regions) or the Western Palearctic. ‘Plants and plant products’ served as the main introduction pathway, yet the commodities involved varied depending on the region they were imported from. We found that parasitoid families were less specialized in their commodity associations than other insect families. Most of the insects identified to species-level were host generalists, and most of the species that have not established in the USA have known hosts present.

While the initial arrival and establishment of non-native predators and parasitoids generally goes unnoticed, unintentional introductions of such species are clearly occurring at a significant scale globally. For example, 26 % of non-native natural enemy arthropods in New Zealand were introduced unintentionally (Charles, 1998), compared to 66 % in Europe (Roy, Roy and Roques, 2011), and 64 % of non-native parasitoids in North America (Weber *et al.*, 2021). We found that 93 of 194 predator or parasitoid families were intercepted, revealing a diverse array of entomophagous insects transported unintentionally through trade and travel. Increased regulatory restrictions on biological control agents have been implemented in many countries during the last few decades (FAO, 2005; Hajek *et al.*, 2016), and fewer insects are introduced intentionally (Cock *et al.*, 2016; Hajek *et al.*, 2016). In contrast, all the intercepted families, except Euphaeidae (Odonata) and Labiduridae (Dermaptera), were also recorded after 2000 when the USA Plant Protection Act, regulating biological control agents, was implemented (Hunt *et al.*, 2008). The diversity of insect natural enemies arriving suggests the relative importance of accidental biocontrol may be growing.

The most frequently intercepted orders were Coleoptera, Hemiptera and Hymenoptera, all among the insect taxa with the highest number of described species globally (Stork, 2018). Diptera are also highly diverse yet represented less than 2 % of interceptions. Liebhold *et al.* (2016)

similarly found that Diptera were consistently under-represented in non-native insect assemblages worldwide. Differences in life history, body size, ecology, and behaviour influence species' probability of entering and surviving human-mediated dispersal, as well as detection during inspections (Liebhold *et al.*, 2016; Gippet *et al.*, 2019; Mally *et al.*, 2022). The low number of Diptera interceptions may be explained in part by these factors.

Overall, only a fraction of transported insects are actually intercepted (Chen, Epanchin-Niell and Haight, 2018; Turner *et al.*, 2021). Due to the biosecurity focus on plant pests (Saccaggi *et al.*, 2016) it is likely that fewer entomophagous insects are recorded, and fewer still are likely to be identified to species-level. We have therefore probably underestimated the diversity of transported natural enemies. Nevertheless, the main introduction pathways, origins, and trends in host specificity identified are likely to be robust. It is also likely that many parasitoids are not discovered during inspections as they are difficult to detect as larvae in their hosts, or as relatively tiny adults among transported commodities. Once a quarantine pest is established, new arrivals of the species may not be prioritized or recorded during inspections, but may provide a pathway of entry for parasitoids. Furthermore, a large fraction of parasitic Hymenoptera are undescribed (Forbes *et al.*, 2018), and this under-developed taxonomy often prevents accurate characterization of intercepted species.

The chances of natural enemies successfully establishing are higher if their host is already present in large numbers. It can therefore be expected that host species tend to establish first, followed by their natural enemies, the so-called receptive bridgehead effect (Weber *et al.*, 2021). Most of the transported species that have not established in the USA are either generalist predators, or parasitoids with at least one known host present, which could facilitate establishment if successfully introduced in the future. Of the 147 species that are currently not established in the USA, 37 have already established elsewhere outside their native range. *Vespula vulgaris*, *Ropalidia marginata* and *Polistes chinensis* (Hymenoptera: Vespidae) are further listed as invasive, and might cause similar damage if they eventually establish in the USA. More positively, 39 intercepted species have been intentionally introduced or studied as potential biocontrol agents internationally, and could potentially also control pests in the USA.

The movement of plants and plant products is a well-known pathway for plant pest introductions worldwide (Liebhold *et al.*, 2012; Meurisse *et al.*, 2019; Fenn-Moltu *et al.*, 2022), and our analysis indicates that this pathway is similarly important for predators and parasitoids. Nonetheless, a broad range of commodity types were implicated, justifying continued biosecurity measures for alternative pathways. The commodities involved also varied depending on their origin. For instance, the plants and plant products with the most interceptions were 'fruit and nuts' exported from the Panamaian region, and 'live plants and cut flowers' from the Western Palearctic (Figure 4b). Interceptions with tiles represented an important pathway from the Western Palearctic (Figure 4a). Marble and ceramic tiles have previously been implicated in insect transport to the USA (Work *et al.*, 2005; Haack, 2011; Fenn-Moltu *et al.*, 2022), likely due to extended periods of storage outside, providing favourable harbourage for hitchhikers.

Predatory Hymenoptera that were frequently associated with inorganic commodities (Figure 5) could potentially be transported as entire nests or aggregations (e.g., Vespidae and Sphecidae, respectively), subsequently facilitating their establishment. We found that parasitoid families were generally less specialized in their commodity associations than other insect families. Related species may parasitise a variety of different insects, which in turn may be transported with a broad range of commodities. Furthermore, adult parasitoids may be generalized nectar foragers (Zemenick *et al.*, 2019), thereby contaminating a variety of plant products. Conversely, the four most frequently intercepted parasitoid species were more specialized in their commodity associations than predator species, mainly arriving with 'live plants and cut flowers', 'coffee, tea, herbs, and spices', and 'cereals'. Over half of natural enemy insects were imported from within the Americas, alongside a considerable number from the Western Palearctic. This is likely driven by patterns of historical plant imports to the USA, dominated by Central America and Europe (MacLachlan *et al.*, 2021). The global trade network is continuously evolving however (He and Deem, 2010). As the sources and types of commodities imported shift, the community of insects arriving will likely follow suit.

Biological control agents are often collected in limited numbers from a few sites (DeBach and Rosen, 1991), followed by further loss of genetic diversity due to mortality in transit and inbreeding during mass-rearing (Woodworth *et al.*, 2002; Franks, Pratt and Tsutsui, 2011). In contrast, while accidental introductions can stem from just a few individuals from a single population (e.g., Arca *et al.*, 2015), large initial propagule sizes and multiple introductions are common (Garnas *et al.*, 2016). We observed that almost a third of natural enemy species were intercepted with commodities imported from more than one country, and 22 % from more than one region. Multiple introductions from genetically distinct populations may increase genetic diversity in the non-native range (Gaudeul *et al.*, 2011; Müller-Schärer, Sun and Schaffner, 2023). Genetic admixture once introduced can further increase standing genetic diversity, create heterosis (hybrid vigour), and potentially enhance species' ability to adapt to new conditions (Kolbe *et al.*, 2008; Szűcs *et al.*, 2012; Müller-Schärer, Sun and Schaffner, 2023).

We found that 82.7 % of transported species were host generalists. Generalist natural enemies have a complex ecological role, feeding on herbivores, predators, detritivores, and plants (Polis and Strong, 1996; Snyder and Evans, 2006), and parasitising a range of hosts (Peters, 2011). Generalists may also have greater establishment success (Weber *et al.*, 2021), and are more likely to have impacts on invaded communities (Louda *et al.*, 2003; Crowder and Snyder, 2010). The diet of insect predators is generally less specialized than many herbivores; while some taxa feed on a few related species, many attack any prey within a size-range they can physically manage (Hurd, 2008). Likewise, even relatively specialized parasitoids occasionally attack other species, and non-native parasitoids acquiring novel hosts may be common (Parry, 2009).

The high proportion of host generalists, and the diversity of families arriving, highlights the importance of continued research into accidental biocontrol due to the increased potential for risks associated with generalists. With a few exceptions (e.g., *Harmonia axyridis*), the impacts of accidentally introduced biological control agents have not been studied, despite the considerable potential for impacts. Given the sheer volume of goods and people transported globally it is unrealistic to prevent all new invasions, but biosecurity measures can reduce the rates at which species arrive and establish (Magarey, Colunga-Garcia and Fieselmann, 2009; Leung *et al.*, 2014). Improved phytosanitary practices should be associated with pathways that are particularly likely to result in new accidental biocontrol introductions. Another option would be including the risk of natural enemy introductions in risk assessments evaluating the need for import restrictions. These changes could help to shift the balance from unintentional toward intentional, evidence-based importation biological control. However, unintentional insect introductions will likely increase in the future, natural enemies included (Seebens *et al.*, 2017). A deeper understanding of the mechanisms driving establishment of non-native parasitoids and predators can help to detect, avoid, and manage their negative impacts while benefiting from the positive ones.

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Conflict of interest: the authors declare no conflict of interest.

Supplementary material: chapter 3

Curation of border interception records

Interception records from 1913-1984 were digitized from paper records published annually by the US Department of Agriculture; see Turner *et al*. (2020) for a description. Records from 1998-2018 were obtained from the USDA Agricultural Quarantine Activity System database which records discoveries of organisms during inspections by the US Department of Homeland Security, Customs and Border Protection, and USDA APHIS PPQ at US ports of entry (Kim *et al*., 2019). There is a break from 1985-1997 in the records we analysed, and there were no insect predators or parasitoids recorded in 13 of the years prior to 1965. Inspections are conducted for imported land, sea and air cargo, incoming passenger baggage, ships stores and mail and parcel post.

We standardized insect taxonomic names according to the Global Biodiversity Information Facility backbone taxonomy (GBIF Secretariat, 2019) using the ‘taxize’ (Chamberlain and Szöcs, 2013) and ‘rgbif’ R packages (Chamberlain *et al.*, 2021)**.** We standardised commodity descriptions according to the international Harmonized Commodity Description and Coding System (HS) for traded goods (World Customs Organization, 2021), and subsequently grouped commodities into broad classes based on the type of product (Table S2). The HS is a hierarchical system of six-digit codes, where the first two digits (HS-2) identify the chapter that a commodity belongs to (e.g., HS 08: ‘Fruit and nuts, edible; peel of citrus fruit or melons’). Analyses of commodity associations were carried out at the level of HS-2 commodities.

Species’ host specificity

While definitions of ‘specialists’ or ‘generalists’ vary considerably in the literature (e.g., Henneman and Memmott, 2001; da Silva and Jaffe, 2002; Frank and Gillett-Kaufman, 2006), we chose definitions that allow us to separate host or prey range into informative categories. We used the Global Biotic Interactions database (Poelen, Simons and Mungall, 2014) to identify known hosts of intercepted species, and supplemented these host association data with internet searches for the species’ taxonomic name and the keyword ‘host’ for parasitoids or the keywords ‘diet’, ‘prey’, ‘feeding’ and ‘predator’ for predators. There may be differences between the range of possible host or prey species (fundamental host range), and the subset of species that are actually used under field conditions (ecological host range) depending on the insects’ habitat use, life history and behaviour (Müller-Schärer, Sun and Schaffner, 2023). We chose to classify species’ fundamental host range because records of prey or host associations under field conditions were frequently unavailable. However, this could be an overestimation for some insects. For example, the butterfly *Pieris virginiensis* (Lepidoptera: Pieridae) is a suitable host for *Cotesia* parasitoid wasps (Hymenoptera: Braconidae) in laboratory tests, but it is a strictly woodland species and the wasps do not forage in closed woodland (Louda *et al.*, 2003). Additionally, recorded use of hosts or prey is not evidence in itself for an adverse impact on their population (Louda *et al.*, 2003).

Species' invasion status

We recorded which of the transported species were established in the USA, or elsewhere in the world based on the International Non-native Insect Establishment Data (Turner, Blake and Liebhold, 2021) and the Global Species First Records Database (Seebens *et al*., 2017). We established whether the species were introduced intentionally as biological control agents, and whether they are considered as invasive in the USA based on the United States Register of Introduced and Invasive Species (US-RIIS) (Simpson *et al*., 2022). We recorded whether they are listed as invasive globally based on the Global Register of Introduced and Invasive Species (Pagad *et al*., 2022). To determine if the insects were introduced, or have been studied as potential biological control agents, outside of the USA we carried out internet searches for the species taxonomic name with the keywords 'biocontrol' and 'biological control'. We did not consider species used for augmentative biological control within their native range as biocontrol agents in this context.

Table S1. insect families largely or entirely comprising predator or parasitoid species.

Order	Family	Type
Coleoptera	Anthicidae	Predator
Coleoptera	Cantharidae	Predator
Coleoptera	Carabidae	Predator
Coleoptera	Cleridae	Predator
Coleoptera	Coccinellidae	Predator
Coleoptera	Cucujidae	Predator
Coleoptera	Cybocephalidae	Predator
Coleoptera	Dytiscidae	Predator
Coleoptera	Gyrinidae	Predator
Coleoptera	Histeridae	Predator
Coleoptera	Hydrophilidae	Predator
Coleoptera	Hygrobia	Predator
Coleoptera	Lampyridae	Predator
Coleoptera	Lycidae	Predator
Coleoptera	Melyridae	Predator
Coleoptera	Monotomidae	Predator
Coleoptera	Noteridae	Predator
Coleoptera	Passandridae	Parasitoid
Coleoptera	Rhipiceridae	Parasitoid

Coleoptera	Ripiphoridae	Parasitoid
Coleoptera	Salpingidae	Predator
Coleoptera	Staphylinidae	Predator
Coleoptera	Thanerocleridae	Predator
Coleoptera	Trogossitidae	Predator
Dermaptera	Labiduridae	Predator
Diptera	Phaeomyiidae	Predator
Diptera	Scathophagidae	Predator
Diptera	Therevidae	Predator
Diptera	Acroceridae	Parasitoid
Diptera	Asilidae	Predator
Diptera	Bombyliidae	Parasitoid
Diptera	Chamaemyiidae	Predator
Diptera	Chaoboridae	Predator
Diptera	Conopidae	Parasitoid
Diptera	Cryptochetidae	Parasitoid
Diptera	Dolichopodidae	Predator
Diptera	Empididae	Predator
Diptera	Megamerinidae	Predator
Diptera	Nemestrinidae	Parasitoid
Diptera	Pipunculidae	Parasitoid
Diptera	Pyrgotidae	Parasitoid
Diptera	Sciomyzidae	Parasitoid
Diptera	Tachinidae	Parasitoid
Diptera	Xylophagidae	Predator
Emphemoptera	Ephemeridae	Predator
Hemiptera	Anthocoridae	Predator
Hemiptera	Dipsocoridae	Predator
Hemiptera	Geocorinae	Predator
Hemiptera	Gerridae	Predator
Hemiptera	Hebridae	Predator
Hemiptera	Nabidae	Predator
Hemiptera	Naucoridae	Predator
Hemiptera	Nepidae	Predator
Hemiptera	Notonectidae	Predator
Hemiptera	Pleidae	Predator
Hemiptera	Reduviidae	Predator
Hemiptera	Saldidae	Predator
Hemiptera	Subfamily Asopinae	Predator

Hemiptera	Veliidae	Predator
Hymenoptera	Ampulicidae	Predator
Hymenoptera	Aphelinidae	Parasitoid
Hymenoptera	Aulacidae	Parasitoid
Hymenoptera	Austrocynipidae	Parasitoid
Hymenoptera	Bethylidae	Parasitoid
Hymenoptera	Braconidae	Parasitoid
Hymenoptera	Bradynobaenidae	Parasitoid
Hymenoptera	Ceraphronidae	Parasitoid
Hymenoptera	Chalcididae	Parasitoid
Hymenoptera	Crabronidae	Predator
Hymenoptera	Diapriidae	Parasitoid
Hymenoptera	Dryinidae	Parasitoid
Hymenoptera	Embolemidae	Parasitoid
Hymenoptera	Encyrtidae	Parasitoid
Hymenoptera	Eucharitidae	Parasitoid
Hymenoptera	Eulophidae	Parasitoid
Hymenoptera	Eupelmidae	Parasitoid
Hymenoptera	Evaniidae	Parasitoid
Hymenoptera	Figitidae	Parasitoid
Hymenoptera	Ibaliidae	Parasitoid
Hymenoptera	Ichneumonidae	Parasitoid
Hymenoptera	Leucospidae	Parasitoid
Hymenoptera	Liopteridae	Parasitoid
Hymenoptera	Maamingidae	Parasitoid
Hymenoptera	Megalyridae	Parasitoid
Hymenoptera	Megaspilidae	Parasitoid
Hymenoptera	Monomachidae	Parasitoid
Hymenoptera	Mutillidae	Parasitoid
Hymenoptera	Mymaridae	Parasitoid
Hymenoptera	Mymarommatidae	Parasitoid
Hymenoptera	Ormyridae	Parasitoid
Hymenoptera	Orussidae	Parasitoid
Hymenoptera	Perilampidae	Parasitoid
Hymenoptera	Platygastridae	Parasitoid
Hymenoptera	Pompilidae	Predator
Hymenoptera	Proctotrupidae	Parasitoid
Hymenoptera	Pteromalidae	Parasitoid
Hymenoptera	Rhopalosomatidae	Parasitoid

Hymenoptera	Rotoitidae	Parasitoid
Hymenoptera	Scelionidae	Parasitoid
Hymenoptera	Sclerogibbidae	Parasitoid
Hymenoptera	Scolebythidae	Parasitoid
Hymenoptera	Scoliidae	Parasitoid
Hymenoptera	Sierolomorphidae	Parasitoid
Hymenoptera	Signiphoridae	Parasitoid
Hymenoptera	Sphecidae	Predator
Hymenoptera	Stephanidae	Parasitoid
Hymenoptera	Tetracampidae	Parasitoid
Hymenoptera	Thynnidae	Parasitoid
Hymenoptera	Tiphiidae	Parasitoid
Hymenoptera	Torymidae	Parasitoid
Hymenoptera	Trichogrammatidae	Parasitoid
Hymenoptera	Trigonalidae	Parasitoid
Hymenoptera	Vespidae	Predator
Lepidoptera	Cyclotornidae	Parasitoid
Lepidoptera	Epipyropidae	Parasitoid
Mantodea	Chaeteessidae	Predator
Mantodea	Acanthopidae	Predator
Mantodea	Amelidae	Predator
Mantodea	Amorphoscelidae	Predator
Mantodea	Angelidae	Predator
Mantodea	Chroicopteridae	Predator
Mantodea	Coptopterygidae	Predator
Mantodea	Dactylopterygidae	Predator
Mantodea	Deroplatyidae	Predator
Mantodea	Empusidae	Predator
Mantodea	Epaphroditidae	Predator
Mantodea	Eremiaphilidae	Predator
Mantodea	Galinthiadidae	Predator
Mantodea	Gonypetidae	Predator
Mantodea	Haaniidae	Predator
Mantodea	Hoplocoryphidae	Predator
Mantodea	Hymenopodidae	Predator
Mantodea	Iridopterygidae	Predator
Mantodea	Leptomantellidae	Predator
Mantodea	Liturgusidae	Predator
Mantodea	Majangidae	Predator

Mantodea	Mantidae	Predator
Mantodea	Mantoididae	Predator
Mantodea	Metallyticidae	Predator
Mantodea	Nanomantidae	Predator
Mantodea	Photinaidae	Predator
Mantodea	Rivetinidae	Predator
Mantodea	Stenophyllidae	Predator
Mantodea	Tarachodidae	Predator
Mantodea	Thespidae	Predator
Mantodea	Toxoderidae	Predator
Megaloptera	Sialidae	Predator
Neuroptera	Ascalaphidae	Predator
Neuroptera	Coniopterygidae	Predator
Neuroptera	Hemerobiidae	Predator
Neuroptera	Mantispidae	Predator
Neuroptera	Myrmeleontidae	Predator
Neuroptera	Osmylidae	Predator
Odonata	Synlestidae	Predator
Odonata	Aeshnidae	Predator
Odonata	Amphipterygidae	Predator
Odonata	Calopterygidae	Predator
Odonata	Chlorocyphidae	Predator
Odonata	Coenagrionidae	Predator
Odonata	Cordulegastridae	Predator
Odonata	Corduliidae	Predator
Odonata	Dicteriastidae	Predator
Odonata	Epiophlebiidae	Predator
Odonata	Euphaeidae	Predator
Odonata	Gomphidae	Predator
Odonata	Hemiphlebiidae	Predator
Odonata	Isostictidae	Predator
Odonata	Lestidae	Predator
Odonata	Lestoideidae	Predator
Odonata	Libellulidae	Predator
Odonata	Megapodagrionidae	Predator
Odonata	Neopetaliidae	Predator
Odonata	Perilestidae	Predator
Odonata	Petaluridae	Predator
Odonata	Platycnemididae	Predator

Odonata	Platystictidae	Predator
Odonata	Polythoridae	Predator
Odonata	Protoneuridae	Predator
Odonata	Pseudolestidae	Predator
Odonata	Pseudostigmatidae	Predator
Plecoptera	Perlidae	Predator
Raphidioptera	Inocelliidae	Predator
Raphidioptera	Raphidiidae	Predator
Strepsiptera	Bahiaxenidae	Parasitoid (endoparasite)
Strepsiptera	Bohartillidae	Parasitoid (endoparasite)
Strepsiptera	Callipharixenidae	Parasitoid (endoparasite)
Strepsiptera	Corioxenidae	Parasitoid (endoparasite)
Strepsiptera	Elenchidae	Parasitoid (endoparasite)
Strepsiptera	Halictophagidae	Parasitoid (endoparasite)
Strepsiptera	Mengenillidae	Parasitoid (endoparasite)
Strepsiptera	Myrmecolacidae	Parasitoid (endoparasite)
Strepsiptera	Stylopidae	Parasitoid (endoparasite)
Strepsiptera	Xenidae	Parasitoid (endoparasite)
Trichoptera	Ecnomidae	Predator

Figure S1. Biogeographic regions of the world as per Holt *et al*. (2013), with the Palearctic region divided into the Eastern and Western Palearctic. The regions were delineated based on the distributions and phylogenetic turnover of amphibian, bird, and mammal species.

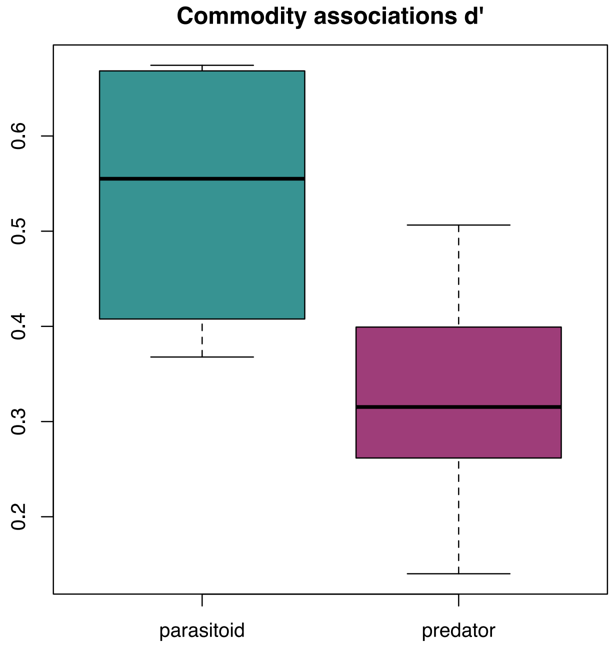

Figure S2: The degree of specialisation (d') in commodity associations for parasitoid (turquoise) and predator (pink) species intercepted ten or more times. d' ranges from 0 (the most generalized) to 1 (the most specialized).

Table S2. The commodity classes that insects were intercepted with. The HS-2 commodity codes included in each class refer to chapters in the international Harmonized Commodity Description and Coding Systems (World Customs Organization, 2021).

Commodity class	**HS-2 codes and full descriptions**
Animal products	01 Animals; live, 02 Meat and edible meat offal, 03 Fish and crustaceans, molluscs and other aquatic invertebrates, 04 Dairy produce; birds' eggs; natural honey; edible products of animal origin, not elsewhere specified or included, 05 Animal originated products; not elsewhere specified or included, 41 Raw hides and skins (other than furskins) and leather, 42 Articles of leather; saddlery and harness; travel goods, handbags and similar containers; articles of animal gut (other than silk-worm gut)
Plant products	06 Trees and other plants, live; bulbs, roots and the like; cut flowers and ornamental foliage, 07 Vegetables and certain roots and tubers; edible, 08 Fruit and nuts, edible; peel of citrus fruit or melons, 09 Coffee, tea, mate and spices, 10 Cereals, 11 Products of the milling industry; malt, starches, inulin, wheat gluten, 12 Oil seeds and oleaginous fruits; miscellaneous grains, seeds and fruit, industrial or medicinal plants; straw and fodder, 13 Lac; gums, resins and other vegetable saps and extracts, 14 Vegetable plaiting materials; vegetable products not elsewhere specified or included, (1111) soil around plants, 53 Vegetable textile fibres; paper yarn and woven fabrics of paper yarn
Foodstuffs	15 Animal or vegetable fats and oils and their cleavage products; prepared animal fats; animal or vegetable waxes, 16 Meat, fish or crustaceans, molluscs or other aquatic invertebrates; preparations thereof,

	17 Sugars and sugar confectionery, 18 Cocoa and cocoa preparations, 19 Preparations of cereals, flour, starch or milk; pastrycooks' products, 20 Preparations of vegetables, fruit, nuts or other parts of plants, 21 Miscellaneous edible preparations, 22 Beverages, spirits and vinegar, 23 Food industries, residues and wastes thereof; prepared animal fodder, 24 Tobacco and manufactured tobacco substitutes
Mineral products	25 Salt; Sulphur; earths, stone; plastering materials, lime and cement, 26 Ores, slag and ash, 27 Mineral fuels, mineral oils and products of their distillation; bituminous substances; mineral waxes
Chemical products	28 Inorganic chemicals; organic and inorganic compounds of precious metals; of rare earth metals, of radio-active elements and of isotopes, 29 Organic chemicals, 30 Pharmaceutical products, 31 Fertilizers, 32 Tanning or dyeing extracts; tannins and their derivatives; dyes, pigments and other colouring matter; paints, varnishes; putty, other mastics; inks, 33 Essential oils and resinoids; perfumery, cosmetic or toilet preparations, 34 Soap, organic surface-active agents; washing, lubricating, polishing or scouring preparations; artificial or prepared waxes, candles and similar articles, modelling pastes, dental waxes and dental preparations with a basis of plaster, 36 Explosives; pyrotechnic products; matches; pyrophoric alloys; certain combustible preparations
Plastics/Rubber	39 Plastics and articles thereof, 40 Rubber and articles thereof
Wood products	44 Wood and articles of wood; wood charcoal, 45 Cork and articles of cork, 46 Manufactures of straw, esparto or other plaiting materials; basketware and wickerwork, 47 Pulp of wood or other fibrous cellulosic material; recovered (waste and scrap) paper or paperboard, 48 Paper and paperboard; articles of paper pulp, of paper or paperboard, 49 Printed books, newspapers, pictures and other products of the printing industry; manuscripts, typescripts and plans
Textiles	50 Silk, 51 Wool, fine or coarse animal hair; horsehair yarn and woven fabric, 52 Cotton, 54 Man-made filaments; strip and the like of man-made textile materials, 56 Wadding, felt and nonwovens, special yarns; twine, cordage, ropes and cables and articles thereof, 57 Carpets and other textile floor coverings, 61 Apparel and clothing accessories; knitted or crocheted, 62 Apparel and clothing accessories; not knitted or crocheted, 63 Textiles, made up articles; sets; worn clothing and worn textile articles; rags
Footwear/Headgear	64 Footwear; gaiters and the like; parts of such articles, 66 Umbrellas, sun umbrellas, walking-sticks, seat sticks, whips, riding crops; and parts thereof
Stone/Glass	68 Stone, plaster, cement, asbestos, mica or similar materials; articles thereof, 69 Ceramic products, 70 Glass and glassware
Metal products	72 Iron and steel, 73 Iron or steel articles, 74 Copper and articles thereof, 75 Nickel and articles thereof, 76 Aluminium and articles thereof, 80 Tin; articles thereof, 81 Metals; n.e.c., cermets and articles thereof, 82 Tools, implements, cutlery, spoons and forks, of base metal; parts thereof, of base metal,

	83 Metal; miscellaneous products of base metal
Machinery/Electrical	84 Nuclear reactors, boilers, machinery and mechanical appliances; parts thereof, 85 Electrical machinery and equipment and parts thereof; sound recorders and reproducers; television image and sound recorders and reproducers, parts and accessories of such articles
Transport vectors and commodities	86 Railway, tramway locomotives, rolling-stock and parts thereof; railway or tramway track fixtures and fittings and parts thereof; mechanical (including electro-mechanical) traffic signalling equipment of all kinds, 87 Vehicles; other than railway or tramway rolling stock, and parts and accessories thereof, 88 Aircraft, spacecraft and parts thereof, 89 Ships, boats and floating structures
Miscellaneous	67 Feathers and down, prepared; and articles made of feather or of down; artificial flowers; articles of human hair, 90 Optical, photographic, cinematographic, measuring, checking, medical or surgical instruments and apparatus; parts and accessories, 91 Clocks and watches and parts thereof, 92 Musical instruments; parts and accessories of such articles, 93 Arms and ammunition; parts and accessories thereof, 94 Furniture; bedding, mattresses, mattress supports, cushions and similar stuffed furnishings; lamps and lighting fittings, n.e.c.; illuminated signs, illuminated name-plates and the like; prefabricated buildings, 95 Toys, games and sports requisites; parts and accessories thereof, 96 Miscellaneous manufactured articles, 97 Works of art; collectors' pieces and antiques

Chapter 4: The influence of feeding guild, host plant diversity, and asexual reproduction on invasion success in thrips

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Abstract

Why some species become invasive is a fundamental question in invasion science. The biotic and abiotic barriers that organisms face along the invasion process, from initial transport, to introduction, establishment, and subsequent spread and impacts, filter species based on their traits. However, attempts to identify traits that are consistently linked to invasion success have been hampered by limited information on the stages of the invasion process occurring prior to establishment. Comparing invasive and native species may not reveal determinants of invasiveness if there is an introduction bias towards species with specific traits that do not play a role in invasiveness. Such comparisons are therefore more informative when combined with a comparison to non-invasive established species (van Kleunen *et al*., 2010). For example, when comparing introduced, established, and widely spreading non-native mammals, Capellini *et al*. (2015) found that species with certain traits were more likely to be introduced, meaning that human-mediated dispersal considerably biased which species have the opportunity to become invasive. Here we use thrips (Insecta, Thysanoptera) as a model system test if certain feeding guilds, diversity of host plants used, and reproductive mode are over-represented at different stages of the invasion process. We used a unique dataset of 151,7490 historical border interception records from eight regions between 1914 and 2019 to characterize the pool of species that are transported but have not successfully established. We combined these data with records of successfully established non-native thrips, and data on species with documented negative impacts. Characterising the pool of species that have succeeded or failed at different invasion stages can inform effective biosecurity practices and limit future invasions. We found that herbivores were over-represented, and fungivores under-represented among all non-native thrips compared to the global species pool. There was an increasing proportion of species with the capacity for asexual reproduction at progressive invasion stages (transport, establishment, invasion). While only a small proportion of thrips have documented negative impacts to date, the majority of non-native thrips were polyphagous herbivores. The pool of species that are arriving in new regions, or have already established outside their native range, may include several future pest species with potential for considerable ecological impacts.

Introduction

Globalization facilitates the spread of species outside of their historical range (Meyerson and Mooney, 2007; Seebens *et al.*, 2018). As the rate of species introductions continues to rise, the costs associated with invasive species and their management have escalated concurrently (Colautti, Grigorovich and MacIsaac, 2006; Diagne *et al.*, 2021). Moreover, invasive species are tied to biodiversity loss (Roy *et al.*, 2023), and can negatively affect human well-being (Jones, 2017; Ogden *et al.*, 2019). Identifying the drivers of invasion success is therefore of critical importance for implementing efficient biosecurity policies and limiting the impacts of future species introductions (Hulme *et al.*, 2008). Determining why some species become invasive, while others establish without negative impacts, or are never introduced in the first place, is a fundamental question in invasion science. Abiotic and biotic barriers filter species as they progress along the invasion process (transport, introduction, establishment, spread and impacts), and these barriers will potentially select for different traits depending on the stage (Gippet *et al.*, 2019). While searching for predictors of invasiveness has been a major line of research in invasion biology since Baker (1965) listed the traits of the “ideal weed”, the results so far have been rather idiosyncratic (Pyšek and Richardson, 2007). This may in part be due to a confounding relationship with propagule pressure for many of the traits considered (Lockwood, Cassey and Blackburn, 2005), but identifying traits linked to invasion success has also been hampered by a lack of information about the processes occurring prior to species successfully establishing in a new area.

Potentially influential traits are generally identified by comparing assemblages of non-native versus native species, or invasive versus established non-native species (van Kleunen *et al.*, 2010). However, this approach does not discriminate between traits that are common among non-native species because they improve establishment success, and traits that were already common among the pool of species that were transported and successfully introduced (van Kleunen *et al.*, 2010; Capellini *et al.*, 2015). Here we use thrips (order Thysanoptera) as a model taxon to study the importance of species traits for success at different invasion stages. Thrips are minute, ubiquitous, cryptic and mobile insects, occupying widely disparate niches and displaying a diverse array of lifestyles (Morse and Hoddle, 2006). While most thrips are phytophagous, living and feeding on a variety of plants and plant parts, others inhabit leaf litter, dead wood or bark and feed on fungal spores or hyphae. Some thrips are either obligate or facultative predators of mites, whiteflies, coccids, and other thrips (Ananthakrishnan, 1979), and a few are even parasites (e.g., Mendonça, Cavalleri and Kaminski, 2012). Invasive Thysanoptera, like the western flower thrips (*Frankliniella occidentalis)* feeding on over 500 different plants, or the onion thrips (*Thrips tacabi*) found on all continents except Antarctica, have become infamous for the damage they cause to agricultural crops around the world. A few species, all in the Thripinae subfamily, are also vectors of plant viruses that do considerable damage to vegetable, field and ornamental crops (Jones, 2005). The presence of widespread, notorious invaders, and the wide variety of traits and lifestyles represented, make Thysanoptera an ideal taxon to study the importance of species traits for invasion success.

The earlier stages of unintentional insect introductions are usually not observed. However, many countries carry out inspections of imported cargo, passenger baggage, and mail, and thus maintain records of the insect species detected at their borders. Such interception records offer valuable insight into the generally overlooked processes occurring prior to unintentional establishments (Turner *et al.*, 2021). To describe the pool of transported species, we used a unique dataset of 151,7490 interceptions of thrips species detected during border inspections in Australia, Canada, mainland USA, Hawaii, Japan, South Africa, Europe, and the United Kingdom, between 1914 and 2019. Combining these records of transported thrips with comprehensive country lists of established, and invasive, non-native species allows us to characterise the pool of species that have succeeded or failed at each stage, and thereby identify shared traits linked to invasion success.

Traits frequently suggested to promote invasion success include those favouring rapid reproduction, good dispersal ability, and a generalist diet (Kolar and Lodge, 2001; Pyšek and Richardson, 2007; Hayes and Barry, 2008; Peacock and Worner, 2008; Allen, Street and Capellini, 2017). Feeding habits in particular are often associated among non-native insect assemblages (Mondor, Tremblay and Messing, 2007; Liebhold *et al.*, 2016; Lantschner, Corley and Liebhold, 2020). About half of known thrips species feed on fungi, around 40 % feed on the living tissues of dicotyledonous plants or grasses, and the remainder exploit mosses, ferns, gymnosperms, or cycads, or are predators or parasites of other small arthropods (Mound and

Teulon, 1995; Morse and Hoddle, 2006). Obligate predation occurs in unrelated genera, including Scolothrips (Thripidae), Karnyothrips (Phlaeothripidae), and Franklinothrips (Aeolothripidae), and facultative predation is widespread (e.g., *Aeolothrips* spp., *Thrips tabaci*, *Frankliniella schultzei*) (Mound, 2005). Secondly, species with generalist habits may more easily find suitable conditions for establishment. For example, Scolytinae (Coleoptera) that are both polyphagous and sib-mating are over-represented among non-native species (Lantschner, Corley and Liebhold, 2020). The range of host plants used by thrips varies from strict monophagy to extensive polyphagy, often within the same genus. While studies of thrips behaviour and resource use are complicated by their small size, mobility, and cryptic habits, the range of plants that a species interacts with can indicate their host- and habitat generalism in a broad sense. Lastly, to establish a population, individuals must be able to successfully reproduce. The capacity for asexual reproduction has widely been used to assess invasion risk in plants, and has been suggested as a driver of invasion success across taxa (Emiljanowicz, Hager and Newman, 2017; Queffelec *et al.*, 2021). The theoretical benefits of asexual reproduction for non-native species are clear: it allows a single individual to colonize a new area, increases population growth rates, and allows for the transmission of locally adapted genotypes without alteration (Bazin *et al.*, 2014). While the importance of asexual reproduction for invasions has largely been discussed in the context of taxa where an asexual form has become invasive (Tabata *et al.*, 2016; Rubio-Meléndez *et al.*, 2019; Queffelec *et al.*, 2021), it remains unclear if this pattern holds across species or is due to introduction bias.

Propagule pressure (the number of individuals introduced to an area; Williamson, 1996; Lockwood, Cassey and Blackburn, 2005) and colonization pressure (the number of species introduced to an area; Lockwood, Cassey and Blackburn, 2009; Blackburn, Cassey and Duncan, 2020) are key determinants of invasion success across taxa. Nonetheless, considerable unexplained variation in establishment success remains after accounting for propagule pressure (Capellini *et al.*, 2015). The influential “tens rule” hypothesis claims that around 10 % of species will successfully make it through consecutive steps of the invasion process: ~10 % of transported species are introduced, ~10 % of introduced species are able to establish, and ~10% of established species become invasive (Williamson, 1996). In this study we have used border interception records, alongside lists of established, and invasive, thrips, to compare the traits of species that have succeeded or failed at transitions along the invasion process. We further describe the main introduction pathways, and test whether the 'tens rule' hypothesis applies for non-native thrips.

Methods

Pools of native, transported, established, and invasive species

We collated data on 6311 thrips species from the ThripsWiki checklist (2022), including synonyms and records of species' feeding guild. We used this species list, and the associated records of feeding guilds, to represent the global pool of Thysanoptera. We used historical border interception records in Australia, Canada, mainland USA, Hawaii, Japan, South Africa, Europe (EPPO member states) and the United Kingdom between 1914 and 2019 to identify transported species. The data consist of insect interceptions at air, land and maritime ports collected during inspections of international air and sea cargo, mail, vessels, and passenger baggage arriving at ports of entry (i.e., land borders, air and sea ports and transitional facilities) as part of national biosecurity programmes (Saccaggi *et al*., 2016; Black and Bartlett, 2020).

We compiled a list of Thysanoptera species that have established outside of their native range based on the International Non-native Insect Establishment Data (Turner, Blake and Liebhold, 2021) and the Alien Species First Records database (Seebens *et al.,* 2020). We then determined whether species were considered to be invasive based on the Global Register of Introduced and Invasive Species (GRIIS) (Pagad *et al.,* 2022), the United States Register of Introduced and Invasive Species (US-RIIS) (Simpson *et al*., 2022), and the Thripidae pests listed by Mound *et al*. (2022) as 'frequently a pest' or 'orthotospovirus vector' (excluding *Enneothrips flavens* which is likely a misidentification (Lima *et al*., 2022)). We harmonized all species taxonomic names using ThripsWiki as a reference (ThripsWiki, 2022).

Capacity for parthenogenesis

We recorded whether thrips species were known to reproduce asexually based on Van Der Kooi, Matthey-Doret and Schwander (2017) and Woldemelak (2021), and completed the list with additional internet searches using the species taxonomic name and the keyword 'parthenogenesis'. We did not distinguish between species reproducing by obligate or facultative parthenogenesis, and were not able to determine whether the non-native species recorded have originated from an asexually reproducing population or not. We also noted whether males of each species have been described in the literature. We assumed that a species reproduces sexually unless known to do otherwise. Hence, the prevalence of parthenogenesis is almost certainly underestimated due to the limited research on reproduction in thrips, which is particularly true for the pool of native species where many are not well studied.

Feeding guild and plant diversity

We used the information on species' feeding guild from ThripsWiki (2022) to characterise the global species pool. For the non-native species, we gathered additional data on feeding habits based on specialised websites including Oz Thrips (Mound, Tree and Paris, 2023), thrips.net (Moritz, 2023), Thrips of California (Hoddle, Mound and Paris, 2012), Thrips of the British Isles (Mound, Collins and Hastings, 2018), TreatmentBank (Plazi, 2023), Plant Parasites of Europe (Ellis, 2023) and relevant literature from Google Scholar searches using the taxonomic name and the keywords 'host', 'plant', 'feeding', and 'breeding'. We recorded which feeding guild each species belongs to (herbivore, fungivore, predator, parasitoid, or some combination of the former), and, where available, the specific plants and plant parts they feed and breed on. We classed parasitoids and species belonging to more than one feeding guild as 'mixed' due to the low number of species in these categories. For fungivores we did not distinguish between feeding on fungal hyphae and on fungal spores.

We then categorised the diversity of plants each species interacts with, defining species as monophagous (found on plants from one genus), stenophagous (found on plants from one family), oligophagous (found on plants from one order), or polyphagous (found on plants from multiple orders). While this categorisation is generally applied for feeding habits alone, we have applied the same categories to all plant-thrips interactions. It was not generally possible to distinguish between breeding hosts, plants that provide food resources, or plants that were occupied incidentally based on the information available in the literature. It is therefore likely that our plant diversity measure is an overestimation of the true host diversity for many species.

Statistical analysis

We analysed the association between feeding guild and invasion stage for native species, transported species, established species, and invasive species, using a Fisher's exact test with simulated p-values based on 2000 replicates from the 'stats' package (R Core Team, 2023). Fisher's exact test is used to determine if there is a non-random association between two categorical variables. We then compared observed and expected numbers of species in each feeding guild for each of the three non-native stages, calculating the expected number of species assuming an equivalent proportion of species in the native species pool. Bounds about the equivalent proportions were calculated as quantiles of the binomial distribution using the rbinom() function from the 'stats' package (R Core Team, 2023), and species which fell outside these bounds were deemed to be over- or under-represented at the $\alpha = 0.05$ level. We compared the number of species known to have the capacity for asexual reproduction, and species with different degrees of plant use diversity between the three non-native invasion stages using Fisher's exact tests as above. As we lacked information on the reproductive mode and plant use for most native species, we were not able to include this pool of species in all analyses.

Results

There were 444 thrips species detected during border inspections between 1914 and 2019. An additional 110 species have established outside their native range without being intercepted, which results in a total of 554 thrips species that have been successfully transported. The major introduction pathway for thrips was the movement of various 'plants and plant products', which were associated with 99.9 % of interceptions. Most of these interceptions were with 'live plants and cut flowers' (81.1 %), 'vegetables' (11 %), 'fruit and nuts' (3.2 %), 'coffee, tea, herbs and spices' (2.4 %), 'cereals' (1.0 %), and 'seeds, grains and medicinal plants' (1.0 %).

There were records of 281 established non-native species from 68 different countries or islands across Africa, the Americas, Asia, Europe, and Oceania. Nine of these species have been introduced intentionally (Turner, Blake and Liebhold, 2021). There were 41 established thrips species listed as invasive in the databases we queried. We found that 8.7 % of all thrips species are transported, and half of the transported species have been able to establish (50.7 %). Considering the transition directly from native to established, as is often the case in the literature, just 4.5 % of all thrips species have successfully established. Among the established thrips species, 14.6 % have subsequently become invasive with documented negative impacts. The species pools in Figure 1 show the species that have succeeded at a given stage but have failed to pass through the next one, e.g., none of the native species have been recorded outside their native range, none of the transported species have established outside their native range, and none of the established species are considered invasive.

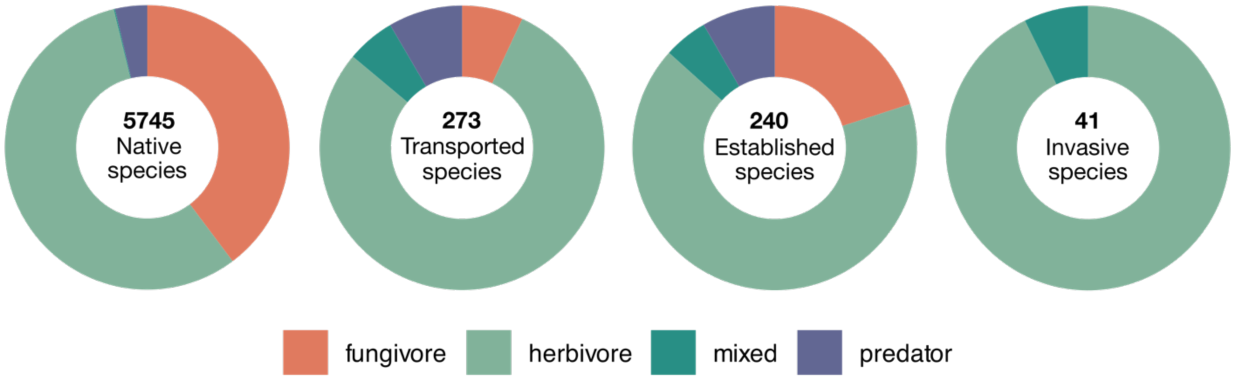

Figure 1. The proportion of thrips species by feeding guild at progressive stages of the invasion process. The pool of species at each stage are those that have not successfully passed through the subsequent stage. Species with 'mixed' diets include herbivore/predators, herbivore/fungivores, fungivore/predators and parasitoids.

There was considerable variation in the proportion of species from each feeding guild across invasion stages (Figure 1). We found that 56.5 % of native thrips species were herbivores, 39.7 % were fungivores, and 3.6 % were predators. Just three native species were known to be both herbivorous and predatory, and five species were parasitoids. For the transported species, 79.1 % were herbivores, 6.9 % were fungivores, 8.4 % were predators, 5.1 % were both herbivorous and predatory, and one species was both predatory and fungivorous. Among the established species, 66.6 % were herbivores, 20.0 % were fungivores, 8.3 % were predators, 4.5 % were both herbivorous and predatory, and one species was both herbivorous and fungivorous. Among the invasive species, 92.7 % were herbivores, while three species were both herbivorous and predatory. We found an overall significant association between invasion stage and feeding guild (Fisher's exact test, $p < 0.001$). Compared to the pool of native species, herbivores were over-represented, and fungivores were under-represented at all three non-native stages.

Just 0.96 % of the 5745 native thrips species were known to have the capacity for asexual reproduction. For the species that were transported but not established this went up to 7.3 %. Among the established species that are not considered invasive, 25.8 % were known to reproduce asexually, and among the invasive species this figure was 51.2 %. There was a significant association between invasion stage (transported, established, invasive) and the number of known asexually reproducing species (Fisher's exact test, $p < 0.001$; Figure 2). Additional species known only from females could potentially be parthenogenetic, or simply not well-studied. If we also assumed these species to be capable of parthenogenesis, the association between stages and reproductive mode remained similar (Fisher's exact test, $p < 0.001$; Figure 2).

Figure 2. The known proportion of asexually reproducing species at progressive stages of the invasion process. Species known to have the capacity for parthenogenesis are shown in blue, species that are only known from females but without records of parthenogenesis found in the literature are shown in turquoise. The remaining species, in green, are assumed to reproduce sexually.

For all three non-native stages, most species were polyphagous in their plant use (61.5 - 82.9 %; Figure 3). There was a significant association between plant use diversity and invasion stage (Fisher's exact test, $p = 0.04$), with a particularly high number of polyphagous invasive species.

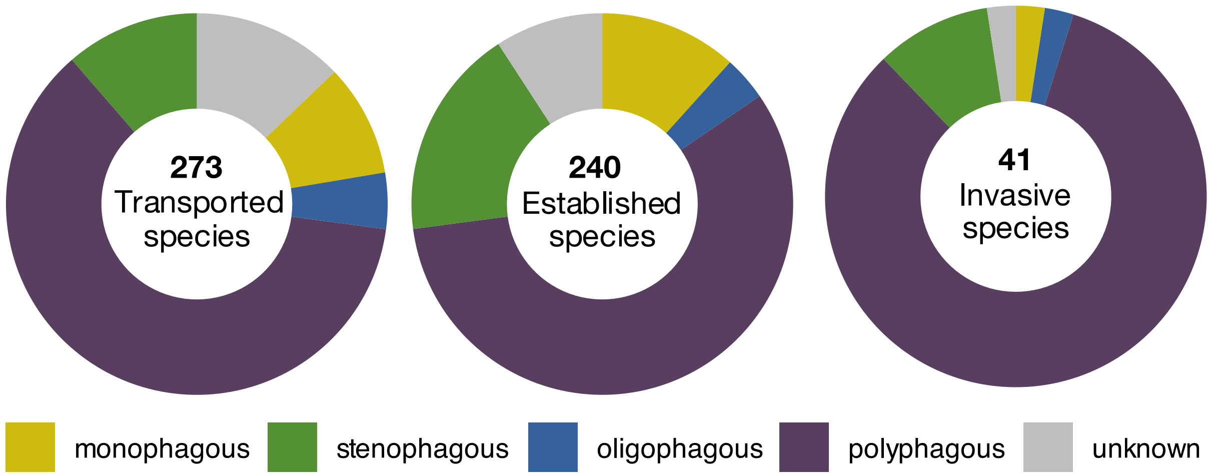

Figure 3. The proportion of thrips species with different levels of plant use diversity at progressive stages of the invasion process. Monophagous species are associated with plants from a single genus, stenophagous species are associated with a single plant family, oligophagous species are associated with a single plant order, and polyphagous species are associated with plants from multiple orders.

Discussion

All three traits varied among the species pools at different invasion stages, highlighting the importance of separating invasive from established species, and accounting for the initial transport stage when describing non-native thrips. We found that herbivorous species were over-represented among the pools of transported, established, and invasive thrips. While fungivores were under-represented overall compared to the pool of native species, the proportion of fungivores was considerably lower among transported than established species. Invasive thrips were either entirely herbivorous, or herbivores with a mixed diet (Figure 1). We found an increasing proportion of species with the capacity for asexual reproduction at each subsequent non-native stage (Figure 2). While most non-native thrips were polyphagous, host plant diversity was significantly associated with invasion stage, and the presence of polyphagous species was more pronounced among the invasive species (Figure 3).

Moreover, it seems that the "tens rule" hypothesis is relevant for thrips introductions. Apart from the transition between transport and establishment, where nearly half of species had been successful, the estimates are close to the 5–20 % interval suggested by Williamson (1996).

Almost all thrips interceptions were associated with various plants and plant products, which likely contributes to the high number of herbivores among all three non-native species pools. If more herbivores are successfully transported and introduced, it follows that more herbivores will also establish due to the greater colonization pressure. It is possible that the high success rate at the transition from transport to establishment is mediated by thrips arriving directly with their host plants, providing many of the resources they require for survival. It has been shown that herbivores tend to establish on their original host plants before potentially switching to native species (Mondor *et al.,* 2007), and may establish more easily following introductions of their hosts (Bonnamour *et al*., 2023). Many non-native thrips were also polyphagous generalists that can utilise a variety of different plants, which would further improve their ability to establish outside their native range.

Only a small number of the plants and plant products being transported internationally are likely to include leaf litter or dead wood, which are the main feeding and breeding sites for fungivorous species. Potential impacts on native ecosystems or agriculture may also be less easily detected for fungivores than for species feeding on plants or animals, thereby contributing to the lack of fungivores at the invasion stage. Predators seem to be similarly represented at the transport and establishment stages compared to the native species pool, but were not present among the invasive species. It is possible that predatory thrips are frequently transported in close association with their prey species, and are thus also frequently introduced with plants and plant products. The potential negative impacts of predators may, similarly to fungivores and other feeding types, be less easily detected as they pose little threat to human interests.

Species traits may also act in synergy. Both herbivory and polyphagy may increase the threat that species pose to agricultural crops, and thereby contribute to the high proportion of polyphagous herbivores among the invasive thrips. There were only a few thrips species listed as invasive overall, and indeed most of the literature on the cost of thrips invasions deals with just four of these species (*Frankliniella occidentalis, Thrips palmi, Thrips tabaci,* and *Scirtothrips dorsalis*) (Kumar *et al*., 2014). It is worth mentioning that the concept of invasive, or pest, species can be considered a socio-economic problem. The perceived negative impacts of any given non-native species will depend on the geographical area, cultivation practices, and market expectations as much as the intrinsic biology of the species (Mound *et al.*, 2022). It may be that the traits of invasive thrips better reflect the threat they pose to human interests than their general invasion success.

We found that the majority of non-native thrips were polyphagous in their plant use. However, the concept of a “host plant” is not easily defined for thrips. Adults are readily observed in the field, but associating adults with their immature stages, and thereby determining their life history and host plant dependencies, is challenging (Mound, 2013). Published host records therefore often include species listed as hosts based on the presence of adults that have dispersed from their breeding site and are casually found on a plant (Mound, 2002). The definition of hosts is further complicated by situations where a plant provides an important feeding or behavioural resource for a species but is not used for breeding. As a consequence, many recorded hosts are merely casual "finding places" with limited biological significance (Mound, 2013). Nonetheless, a strict definition including only host plants where species can successfully maintain a population would exclude plants where they can occasionally produce a few larvae, and would be of limited use for crop protection, for example, where adults might feed on and transmit a pathogen to a plant they cannot breed on (Mound, 2005). In contrast, extending the definition to include all plants that adults are found on, as we have done in this study, may be too broad to be suitable for management purposes (Mound, 2005). The broad diversity of plants species associate with could nonetheless be relevant for thrips invasions as they may also be transported with plants they occupy incidentally.

There can also be geographical variation in host breadth within a species, where polyphagous thrips sometimes produce localized strains with a strong attachment to particular plants. For example, *Scirtothrips aurantii* is highly polyphagous in its native range, but almost entirely restricted to Bryophyllum and a few other Crassulaceae in its non-native range in Queensland, Australia (Mound, 2005). Furthermore, non-native thrips may colonize new hosts in their introduced range, as is the case for many crop pests, and conversely, native thrips have been recorded as colonizing non-native plant species (Mound, 2002). Overall, the large proportion of polyphagous species among non-native thrips infers considerable potential for ecological impacts if, and when, they are able to establish.

Populations of most thrips are bisexual, with sexual reproduction characterized by haplodiploid sex determination (Lewis, 1973). However, partly or wholly parthenogenetic reproduction may be widespread (Ananthakrishnan, 1979), as many species show strongly female-biased population sex ratios or are only known from females (e.g., Lewis, 1973; Mound and Masumoto, 2009). We observed a growing proportion of species with the capacity for asexual reproduction along the invasion stages. It is possible that parthenogenic thrips are more likely to be transported due to high population densities on host plants that are traded commodities, which could also contribute to their likelihood of detection during inspections. It has been suggested elsewhere that parthenogenetic thrips are introduced and spread more easily, and that the absence of males in a population can be a sign of an introduction having taken place (O'Neill and Bigelow, 1964). The increased prevalence of parthenogenesis among established species could be explained by their improved ability to colonize new habitats, through rapid population growth without needing to locate mates. Thrips exhibit various forms of asexual reproduction, including thelytoky (females produced from unfertilized eggs), arrhenotoky (males produced from unfertilized eggs and females produced from fertilized eggs) and deuterotoky (both sexes produced from unfertilized eggs). Additionally, many species have both sexual and parthenogenetic lineages (van Der Kooi, Matthey-Doret and Schwander, 2017). The traits of many species have not been well studied however, and it is likely that many more species are able to reproduce parthenogenetically than we found evidence of in the literature.

Reproductive modes can also differ between and among populations, and can vary over time (Nault *et al*., 2006). Although the mechanisms remain unclear, the geographical distribution of individuals with different reproductive strategies often differs (Silva *et al*., 2020). Asexuality often occurs in habitats that are marginal in some way, either being predominant near the margin of the sexuals' distribution, extending far beyond the sexual range, or disproportionately being found in newly colonizable habitats or habitats where abiotic selection pressures are stronger than biotic ones (Tilquin and Kokko, 2016). We were not able to assign transported species, or indeed records of established species, to a particular native source population with known reproductive mode. It is possible that some of the non-native species we have recorded as asexually reproducing actually derive from sexual populations, potentially inflating our estimates for the non-native stages. Specific breeding experiments or estimates of population sex ratios in the non-native range would be required to accurately determine the reproductive mode of non-native thrips. Moreover, it is likely that non-native species are more thoroughly studied than species remaining in their native range due to the potential for ecological and economic harm that they pose. This could lead to an over-estimation of the prevalence of parthenogenesis among non-native species. However, as we detected a significant association between reproductive mode and invasion stage also when we only considered the three non-native stages (transported, established, and invasive species), the relationship is likely to be robust.

In conclusion, it seems that both feeding guild, plant diversity and reproductive mode are associated with invasion success in thrips. It would be beneficial for future studies to correct for the differences in research effort between species with different invasion histories, potentially using a measure such as the number of publications mentioning the species in question. Currently, only a small proportion of thrips species are considered serious pests (Mound and Teulon, 1995) but unintentional introductions will continue to increase in the future (Seebens *et al.*, 2017). The large numbers of polyphagous herbivores that are already established around the world, and that are being transported and may eventually establish, suggests that many more thrips species could become problematic in the future. While it is unrealistic to prevent all new thrips introductions given the huge volume of plants and plant products being transported globally, biosecurity measures targeting key introduction pathways can reduce the rates at which species arrive and establish (Magarey, Colunga-Garcia and Fieselmann, 2009; Leung *et al.*, 2014). Continued research into the traits of both native and non-native thrips can help us to understand the mechanisms driving invasion success, and thus improve our ability to prevent and manage new introductions.

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Summary of results

Chapter 1: Alien insect dispersal mediated by the global movement of commodities

In this chapter we used a unique dataset of 1,902,392 border interception records from Australia, New Zealand, Europe, Japan, the United States of America, and Canada to identify key commodities associated with insect dispersal through human trade and travel. Using rarefaction and extrapolation methods we estimated the total species richness and diversity associated with different types of commodities. We identified the movement of plant and wood products as the main introduction pathway for insects transported with cargo, passenger baggage, and mail. However, insects were associated with fourteen broad classes of commodities overall, and certain species were mainly transported with specific commodities within these broad categories. Moreover, insects in the same genus tended to share similar commodity associations, potentially informing pathway management of novel non-native species. Pooling border interceptions across regions provided valuable insight into the otherwise unobserved transport stage.

Chapter 2: Global flows of insect transport and establishment: the role of biogeography, trade, and regulations

Non-native species establishments outside of their native range are not evenly distributed geographically, and certain regions of the world are over- or under-represented as donors and recipients of non-native species. To explore the drivers of invasion asymmetry at different stages of the invasion process, we analysed insect border interceptions as a proxy for transported species flows, along with lists of non-native insects established in nine areas. We found that trade intensity had a significant effect on the number of transported and established species, as did their biogeographic origin. Countries with a larger Gross National Income supplied more transported species, and more insects were able to establish when introduced within their native biogeographic region. Our results suggest that accounting for the processes occurring prior to establishment is crucial for understanding invasion asymmetry in insects, and for quantifying regional biosecurity risks.

Chapter 3: Pathways for accidental biocontrol: the human-mediated dispersal of insect predators and parasitoids

While insect introductions for biological control have become more strictly regulated and less frequent in recent decades, the rate of unintentional introductions through human activities is rising. In this chapter we used border interception records from the United States collected over the last century to describe the diversity of entomophagous insects that are transported unintentionally. We found that natural enemy insects from 93 families, representing 11 different orders were arriving at the US border. We identified plants and plant products as their main introduction pathway, and explored trends in host specificity for the natural enemy species that were detected. Two thirds of species were polyphagous host generalists, potentially facilitating their successful establishment. Nearly a third of species arrived with material from more than one country, creating potential for a genetically diverse non-native population. The diverse pool of natural enemy insects we described has potential to cause substantial ecological impacts, both in terms of controlling pests through accidental biocontrol and disrupting native communities.

Chapter 4: The influence of feeding guild, host plant diversity, and asexual reproduction on invasion success in thrips

It is likely that different traits promote species' success at different stages of the invasion process. Here we used records of intercepted, established, and invasive thrips (order Thysanoptera) to investigate the importance of asexual reproduction, host plant diversity, and feeding guild for invasion success. We used records of thrips species intercepted in eight world regions to assess the traits of species that are successfully transported, combined with records of established non-native thrips, and lists of invasive species, to assess the prevalence of traits among the pool of species that succeeded or failed at different invasion stages. We found that herbivores were over-represented among non-native thrips compared to the global species pool, while fungivores were under-represented. Most non-native thrips were polyphagous in their host plant use. Species with the capacity for asexual reproduction were increasingly common at progressive invasion stages (transport, establishment, invasion). The pools of species transported to new regions, or that have already established outside their native range, may include several future pest species with potential for considerable ecological impacts.

General discussion

Biological invasions are part of the profound global changes taking place due to the globalisation of human society under capitalism. Species distributions and patterns of biodiversity are being irreversibly altered through dispersal with human trade and travel, and novel biological communities are arising in almost every ecosystem worldwide. The rate of species introductions continues to accelerate, and many introductions are of species being transported outside of their native range for the first time (Hulme, 2009; Seebens *et al.*, 2017). Indeed, a quarter of species introductions discovered during 2000-2005 have never been previously recorded as non-native anywhere (Seebens *et al.*, 2018). Combined with the uncertainty of climate change, land use change, and ongoing massive biodiversity loss, the long-term consequences of biological invasions remain unclear. And while the field of invasion science is expanding and growing rapidly (Stevenson *et al.*, 2023), the drivers of global invasion patterns are still not well understood. This is particularly the case for taxa that are introduced unintentionally, as they are not actively pre-selected by human preferences, and their global movements generally go unobserved. Insects are among the most widespread, diverse, and economically important non-native organisms in terrestrial ecosystems (Wilson, 1987; Kenis *et al.*, 2009; Renault *et al.*, 2022). They are also typically introduced unintentionally, and are almost ubiquitously present, making them an ideal taxon to study the impacts of globalisation on biological invasions.

Interdisciplinarity between ecological and social sciences is needed to understand and manage the inherently socio-ecological phenomenon of invasions (Vaz *et al.,* 2017). The aim of this thesis was to contribute to our understanding of insect dispersal through global trade, accounting for the mechanisms occurring at different stages of the invasion process: from initial transport and introduction, to establishment, and subsequent spread and impacts. We have used data on the transport and establishment of non-native species to describe the diversity of insects being introduced, and identify major introduction pathways that are relevant across taxa and regions. We have also assessed mechanisms shaping patterns of dispersal with traded commodities, and evaluated the role of species traits for success at different stages of the invasion process. Using a unique dataset of nearly two million border interception records, spanning five continents and over a century, we have been able to explore the otherwise hidden transport stage of insect introductions. We have combined these interception data with comprehensive country-wide lists of established non-native insects, historical trade records, key biogeographic and socio-economic variables, and data on species traits and impacts. The resulting wide taxonomic and geographic spread of the data we analysed have offered an unprecedented insight into insect invasions worldwide.

Overall, we found a huge diversity of insects moving internationally with a wide array of traded commodities. In chapter one we identified plant and wood products as the main commodities transporting a broad range of taxa through cargo, passenger baggage, and international mail. We also found that insects in the same genus tend to share similar commodity associations during transport. In chapter two we showed that both the biogeographic region of origin and trade intensity significantly influenced the number of species being transported and establishing between regions. Countries with higher Gross National Income supplied more transported species, and more species established when introduced within their native biogeographic region. In chapter three we documented the broad diversity of entomophagous insects being transported to the United States during the last century. We found that around a third of predator and parasitoid species arrived with material from more than one country, and that most of these species were polyphagous host generalists. In chapter four we explored the prevalence of feeding guilds and reproductive modes among Thysanoptera at different stages of the invasion process, showing that herbivores were over-represented and fungivores under-represented compared to the global species pool. Asexual reproduction was progressively more prevalent among transported, established, and invasive species, and the majority of non-native thrips were host generalists.

A huge diversity of insects on the move

The border interceptions we analysed in this thesis document the impressive diversity of insects that are inadvertently being transported around the world, with thousands of species identified in the regions we studied. Additionally, a significant proportion of interceptions were not identified to species level, likely concealing an even greater diversity of insects being moved outside their native range. For many insect taxa, a large part of species are also still undescribed (e.g., parasitic Hymenoptera; Forbes *et al.*, 2018), preventing a comprehensive characterization of non-native species. Differences in life history, body size, ecology, and behaviour affect a species' probability of entering and surviving human-mediated dispersal pathways, as well as their likelihood of detection during inspections (Liebhold *et al.*, 2016; Gippet *et al.*, 2019; Mally *et al.*, 2022). Moreover, while biosecurity efforts have largely focussed on herbivorous plant pests (Saccaggi *et al*., 2016; IPPC, 2023), we showed that a considerable number of insects with other feeding habits are also being transported. In chapters two and three we found that many fungivorous and predatory thrips were detected with traded commodities, and there were records of 93 families of entomophagous insects arriving in the USA alone. These non-herbivorous insects represent an understudied pool of non-native species with the potential to cause substantial ecological impacts (e.g., Causton *et al.,* 1006; Snyder and Evans, 2006). The diversity of insects we observed is fuelled by a growing number of native species pools becoming available to human-mediated dispersal (Seebens *et al*., 2018). As trade and travel networks continue to shift and expand, we are likely to experience a concurrent increase in the variety of insects being introduced worldwide, ultimately impacting local ecosystems and economies.

Identifying major introduction pathways

Managing introduction pathways and the corresponding commodities is a potentially powerful strategy for preventing new introductions, but requires knowledge of the specific kind of goods and vectors that insects are associated with during transport. In the light of the many novel species being introduced, it may be more efficient to consider the size and composition of species pools moved along particular pathways, rather than focusing on individual species when assessing establishment risks and mitigation options (Brockerhoff *et al.,* 2014). Knowledge of the exact pathways that unintentionally introduced species arrive by is scarce, but through pooling border interception records across multiple regions we have studied known insect-commodity associations to explore this hidden stage of the invasion process.

Significant progress has been made towards understanding the human-mediated dispersal of certain insect taxa (for example**,** Suarez, Holway and Ward, 2005; Brockerhoff *et al*., 2006; Ward *et al*., 2006; Liebhold *et al*., 2012; Meurisse *et al*., 2019)**,** and the movement of plants and plant products is well-known as a pathway for insect introductions worldwide (Liebhold *et al.*, 2012; Meurisse *et al.*, 2019; Fenn-Moltu *et al.*, 2022). We contributed to this evidence by defining commodity associations for a broad range of insect taxa across geographic regions.

Using rarefaction and extrapolation methods allowed us to estimate the total species richness and diversity associated with different commodity types, including species that were transported without being detected. This is particularly relevant for countries that do not have access to long-term interception records to inform their biosecurity practices.

While imports of plants and plant products were the main introduction pathway for insects overall, in chapter one we showed that a broad range of commodity types were implicated in insect movements, requiring continued biosecurity measures for a range of pathways. For example, we found that textiles, animal products, and foodstuffs transport a particularly high diversity of insects relative to species richness. There were also considerable differences in commodity associations between insect taxa. For instance, we found that species in the same genus tended to share similar commodity associations, but this was not the case within orders or families (Fenn-Moltu *et al.*, 2022). The similarities in commodity associations within genera could potentially inform pathway management for novel non-native species in situations where the introduction pathways of their relatives are known. Further research exploring the degree of similarity in commodity associations within and between taxa would be useful for characterising introduction pathways at different levels of taxonomic generalisation.

Uneven exchanges of non-native insects

The flows of species exchanged between regions are not evenly distributed geographically, with certain regions over- or under-represented as donors and recipients of non-native species (Torchin *et al.*, 2021; van Kleunen *et al.*, 2015; Casado *et al.*, 2018). In chapter two, we showed that this is also the case for non-native insects. A variety of explanations for this invasion asymmetry have been suggested (Jeschke and Genovesi, 2011), but few have been tested empirically. For insects, the most parsimonious explanation is varying opportunities for introduction through trade. However, not all trade is equally likely to lead to new introductions (e.g., Suarez, Holway and Ward, 2005; Liebhold *et al.*, 2012; Fenn-Moltu *et al.*, 2022; Ollier and Bertelsmeier, 2022). More precise trade measures, like import values of commodities known to transport insects, can better represent opportunities for introduction (Ollier and Bertelsmeier, 2022). In chapter two, we used insect interceptions with commodity trade, along with the native ranges of established species, to analyse variables determining the number of species exchanged between biogeographic regions at the transport and establishment stages. We found that the value of commodities imported significantly influenced the species richness moving between regions both during transport and establishment. This result highlights the importance of propagule and colonization pressure for invasion asymmetry in unintentionally introduced organisms. However, the number of transported and established species also varied depending on the insects' biogeographic origin. We found no evidence that this was due to variation in the number of native species available, so it is likely that there are other factors involved. We would require information on the insects' competitive- and colonization abilities, as well as more precisely defined native ranges to determine if there are regional pre-adaptations to invasion success (as per Niemelä and Mattson, 1996). We found some indication that climatic and habitat matching may be important determinants of establishment, which concurs with previous studies (Bomford *et al*., 2009; Capinha *et al*., 2017; Broennimann *et al*., 2021; Trombik *et al*., 2022). More precisely, we found that a greater number of species establish when introduced within their native biogeographic region. Further exploring this association would require more detailed information on the native ranges of non-native insects, which would incidentally also contribute to our understanding of the patterns of richness and diversity for insect assemblages in understudied regions. We also showed that countries with a higher Gross National Income supplied more transported species. This implies that the countries whose actions result in more species introductions are also those that have more financial resources available to address the problem, which is a promising avenue for internalising invasion costs through the 'polluter pays' principle (Hulme, 2015; Perrings *et al.,* 2005). The information available on biological invasions has an uneven global distribution in general, with significant over-representation of particular regions and taxa in the literature (Stevenson *et al*., 2023). A more equitable distribution of research efforts going forwards would lead to a more complete understanding of invasion patterns and processes around the world.

What does it mean to be invasive?

The pool of transported and established insects analysed in this thesis contains several current and potential future invasive species. While we have used a definition of 'invasive' that relies on having documented negative impacts, the term has also been used to describe established species that spread widely or dominate the native community (Pereyra, 2016). However, the degree of spread is likely dependent on both the specific environmental context (With, 2002), the time since introduction (Wilson *et al*., 2007; Ahern *et al*., 2010; Essl, Mang and Moser, 2012), and the natural dispersal ability of the organisms in question (Coutts *et al*., 2011). Moreover, species may be considered as invasive in areas where they have little impact, simply because they were identified as invasive elsewhere (Colautti and MacIsaac, 2004).

As differing perceptions of the harm caused, or benefits gained, by the presence of a particular species are influenced by our human values and management goals, the term invasive can never be entirely neutral. Furthermore, having documented negative impacts necessarily requires someone to take the time and effort to document these impacts. As damages to agriculture, economically important forestry and infrastructure, or human well-being are more likely to be noticed and documented (Renault *et al*., 2022), we can expect that invasive species are biased towards organisms affecting these sectors rather than native communities. Nevertheless, there are already an estimated 7,741 established insect species globally (Zhao *et al*., 2022). This number will almost certainly continue to grow (Seebens *et al*., 2017; Seebens *et al*., 2021), including the subset with devastating ecological impacts (Roy *et al*., 2023). The resources available for managing non-native species are inherently limited, so monitoring systems and interventions must continue to target the insects that are the most problematic for native ecosystems and other human interests. Ideally, management decisions should be based on informed risk analysis that evaluates the potential for long-term, negative effects on ecosystems. This would include the risk of local and global extinctions, potential for damage to ecosystems with cultural significance, as well as risks to food security and human well-being. In this context, clearly distinguishing invasive species with known negative impacts from non-native species that are largely unproblematic for local ecosystems and economies is crucial for efficiently allocating resources.

Identifying potential invasive species

Generalist species may be more easily introduced (Gippet *et al*., 2019), more likely to establish (Chapple, Simmonds and Wong, 2012; Weber *et al*., 2021), and more predisposed to become invasive (Louda *et al*., 2003; Crowder and Snyder, 2010). In chapters three and four, we found support for insects with generalist habits being more likely to be transported initially, to establish successfully, and to eventually be listed as invasive. The high proportion of generalists we observed in the pool of non-native insects, along with the broad diversity of taxa arriving, presents considerable potential for ecological impacts. For thrips in particular, we found that herbivory was the prevalent feeding habit among non-native species, potentially due to the greater likelihood of being introduced along with their host plants. Notably, the invasive thrips were exclusively herbivores, which may reflect the human importance placed on damage to cultivated plants as much as their aptitude for invasion. We also found in chapter four that the capacity for asexual reproduction was increasingly common among transported, established, and invasive thrips. As reproductive modes and host plant use are better studied for non-native than native thrips, it would be helpful for future research to incorporate a measure of research effort when comparing species, for example using the number of published peer-reviewed articles studying each species. Nonetheless, the variation we observed in the representation of different traits between the pools of transported, established, and invasive species highlights the importance of accounting for invasion stage in analyses of traits and invasion success (van Kleunen *et al.*, 2010; Capellini *et al.*, 2015).

Assessing invasion risk in an uncertain future

Both historical and emerging trade dynamics interact to shape the global species exchanges that we observe today and in the future (Epanchin-Niell *et al.*, 2021). Changes to species distributions, the type and volume of commodities being traded, trade partners, regulations, technologies, and biosecurity efforts all influence patterns of human-mediated dispersal. Consequently, the emergence of new trade relationships, commodities, or transport pathways can expand the pool of species that are potentially available for dispersal, creating opportunities for novel introductions (Seebens *et al.*, 2018; Epanchin-Niell *et al.*, 2021). As our ability to predict which species will establish and potentially become invasive is largely based on prior invasion history, the prevalence of species with no previous introductions has important implications for biosecurity. Risk assessment approaches that rely less on invasion history will need to be prioritized (Seebens *et al.*, 2018), warranting a shift towards targeting major introduction pathways, such as the commodities we identified in chapter one, rather than species that are perceived as high-risk.

Insect invasions in a changing climate

Climate change is likely to shift patterns of commodity production and transport, and thus change future invasion dynamics of insects (Hellmann *et al.*, 2008). For example, the opening of Arctic shipping routes as the sea ice melts could considerably reshape and speed up global trade flows (Bekkers, Francois and Rojas-Romagosa, 2018), hence altering the flows of unintentionally transported organisms. Damage to infrastructure and port operations, changes to the economic system, and adaptations in agricultural practices due to extreme weather events and rising temperatures could cause further shifts in regional species exchanges (Dellink *et al.*, 2017). Furthermore, climate change will affect how likely insects are to establish once they have been introduced outside of their native range (Robinet and Roques, 2010; Hulme, 2017). Certain regions may become climatically suitable for species that have been introduced but have so far failed to establish (Hulme, 2017), and warmer temperatures can enable the expansion and damage-potential of already established non-natives (for example, defoliating insects and bark beetles: Netherer and Schopf, 2010; mosquitos: Iwamura, Guzman-Holst and Murray, 2020). A better understanding of introduction pathways and the determinants of invasion success will improve our ability to adapt to these changes going forwards. Moreover, more frequent extreme climatic events could create ecological conditions that both facilitate non-native species establishing and contribute to their spread (Hellmann *et al.*, 2008; Diez *et al.*, 2012). Native communities under climatic stress may have decreased biotic resistance to invasion, disturbed habitats may provide a competitive advantage for non-native species, and at the same time extreme weather events can lead to a greater transport of propagules into new regions (Hellmann *et al.*, 2008). This thesis has contributed to our understanding of historical invasion patterns in insects, which can help to inform the future biosecurity measures required under climate change.

Managing novel insect communities

The rearranging of global biodiversity wrought by the human-mediated dispersal of species is largely irreversible. It is even possible that non-native insects will help to maintain ecosystem functioning in communities where native species are increasingly unable to cope with the rapidly changing climate (McKnight *et al.*, 2021), for example by replacing lost or declining pollinators (Gross, 2001; Dick, Etchelecu and Austerlitz, 2003). However, the presence of certain invasive species is a threat to native ecosystems under stress (Roy *et al*., 2023), and current legislative and scientific tools targeting invasions are likely insufficient to contain the problem (Hulme, 2021). Globally, we will require inter-disciplinary and coordinated efforts to manage the risks posed by invasive species. The effective prevention and management of invasions will require global leadership and coordination, prioritized by all governments, with opportunities for different levels of buy-in depending on national capacities (Meyerson *et al*., 2022). Stronger regional trade regulations, for instance, could help to diminish the risk of introducing invasive species among trading partners at a regional scale (Hulme, 2021).

Finally, previous studies have found a disconnect between research in invasion science and its policy and management applications (Esler *et al*., 2010). This is particularly concerning in light of the limited progress made towards international targets for invasive species management, such as the "partially achieved" Aichi Biodiversity Target number 9, with the goal that "by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated and measures are in place to manage pathways to prevent their introduction and establishment" (Secretariat of the Convention on Biological Diversity, 2020). Now in 2023, there is still a long way to go towards achieving this goal (Roy *et al.,* 2023). Research relating to particular stages of the invasion process could help to integrate research outputs into risk assessments and protocols for prioritizing species management, for example if potentially invasive species can be identified before they cause problems (Richardson and Pyšek, 2012). In summary, containing the risks posed by invasive species will require a global strategy where measures applied at the local and regional scale work together towards the common goal of reducing biological invasions and minimizing their impacts (Meyerson *et al*., 2022).

Conclusions

In this thesis we have explored trends in the human-mediated dispersal of insects using historical border interceptions and lists of established species from different world regions. The unique taxonomic and geographic coverage of these data have allowed us to analyse processes occurring at different stages of the invasion process, and to draw general conclusions that are relevant for global insect movements. We have added to the global knowledge of insect introduction pathways, and have improved our understanding of the factors determining the species richness exchanged between regions. We have documented the massive diversity of insect taxa being dispersed, and have found evidence of traits relevant for successful transport, establishment, and invasion in insects. Studying border interceptions from a variety of regions has been an invaluable tool for analysing global patterns of unintentional human-mediated dispersal. Going forwards, cooperation, communication, and sharing of resources across borders will be essential for managing the impacts of globalisation on biological invasions. The growing threat that invasive species pose towards international biodiversity goals underlines the need for targeted research to support effective understanding, legislation, and management (Stevenson *et al.*, 2023). Taking a risk assessment-based approach to minimising future introductions is crucial, but we will also need to accept that changing biological communities are a part of the ongoing evolutionary processes. Globally, we should aim to manage the pathways and species that pose the greatest threats to biodiversity and functioning ecosystems, while embracing the positive impacts that non-native insects may bring to our changing world.

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