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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 are 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 United States are host generalists or have at least one known host species available. The unintentional transport of diverse natural enemy insects has the potential to cause substantial ecological impacts, both in terms of controlling pests through accidental biocontrol and disrupting native communities. Characterizing the insects being transported and their introduction pathways can inform biosecurity practices and management.

KEYWORDS
accidental biocontrol, border interceptions, human-mediated dispersal, insects, introduction pathways, parasitoids, predators

INTRODUCTION

While most non-native insects go relatively unnoticed, a subset generates negative ecological or economic impacts in its new range (Hill et al., 2016). Indeed, insects are among the most common and damaging animal invaders in terrestrial ecosystems, costing at least US $70 billion 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).

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 (Aukema et al., 2011; Holmes et al., 2009). These invasive herbivores are economically important (Pimentel, 2005), and are the primary focus of most biosecurity measures (Nahrung et al., 2023). Nevertheless, introductions of entomophagous insects are also of considerable importance for both native and non-native biodiversity (Kenis et al., 2009; Louda et al., 2003; Snyder & Evans, 2006).

Releases of entomophagous insects have become integral to pest management around the world (Hajek & 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 & 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) criticized the inherent risks, there have been significant concerns raised about nontarget and indirect effects (e.g., Ewel et al., 1999; Simberloff & Stiling, 1996). 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 of natural enemies for biological control programs 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 & 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, 2007; Barron et al., 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) parasitizing the wheat midge, *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) in North America (Thompson & Reddy, 2016).

All introduced species must overcome a series of biotic and abiotic barriers to establish and spread (Blackburn et al., 2011; Schulz et al., 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 & 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 et al., 2012). Additionally, traits that are advantageous for biological control, such as good dispersal ability, and rapid population growth, may also increase the probability of nontarget 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 programs, screening systems, and early warning strategies (Hulme, 2006). In this paper, we describe the unintentional transport of insect predators and parasitoids to the United States 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 analyzed border interception records collected by US Department of Agriculture and US Department of Homeland Security inspectors between 1913 and 2018 (Appendix S1: Figure S1). 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. 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 (Appendix S1: Table S2). Further details on data sources and cleaning are available in Appendix S1.

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 (Appendix S1: Table S1). Entomophagous species from families where most species have other feeding habits were not included in this study. We further compared families intercepted from 1913 to 2018 with families intercepted from 2000 to 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 & 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 Appendix S1. 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 non-native species 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 well-being. Detailed methods are available in Appendix S1. 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 & 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 et al., 2008) for families intercepted at least 20 times, and for species intercepted at least 10 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 et al., 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 United States versus 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 11 orders (Figure 1). Fifty-two families were intercepted in the period 1913–1999, and all these families, except Euphaeidae (Odonata) and Labiduridae (Dermaptera), were also intercepted in the period after 2000. Thus, 91 families were intercepted from 2000 to 2018. 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.

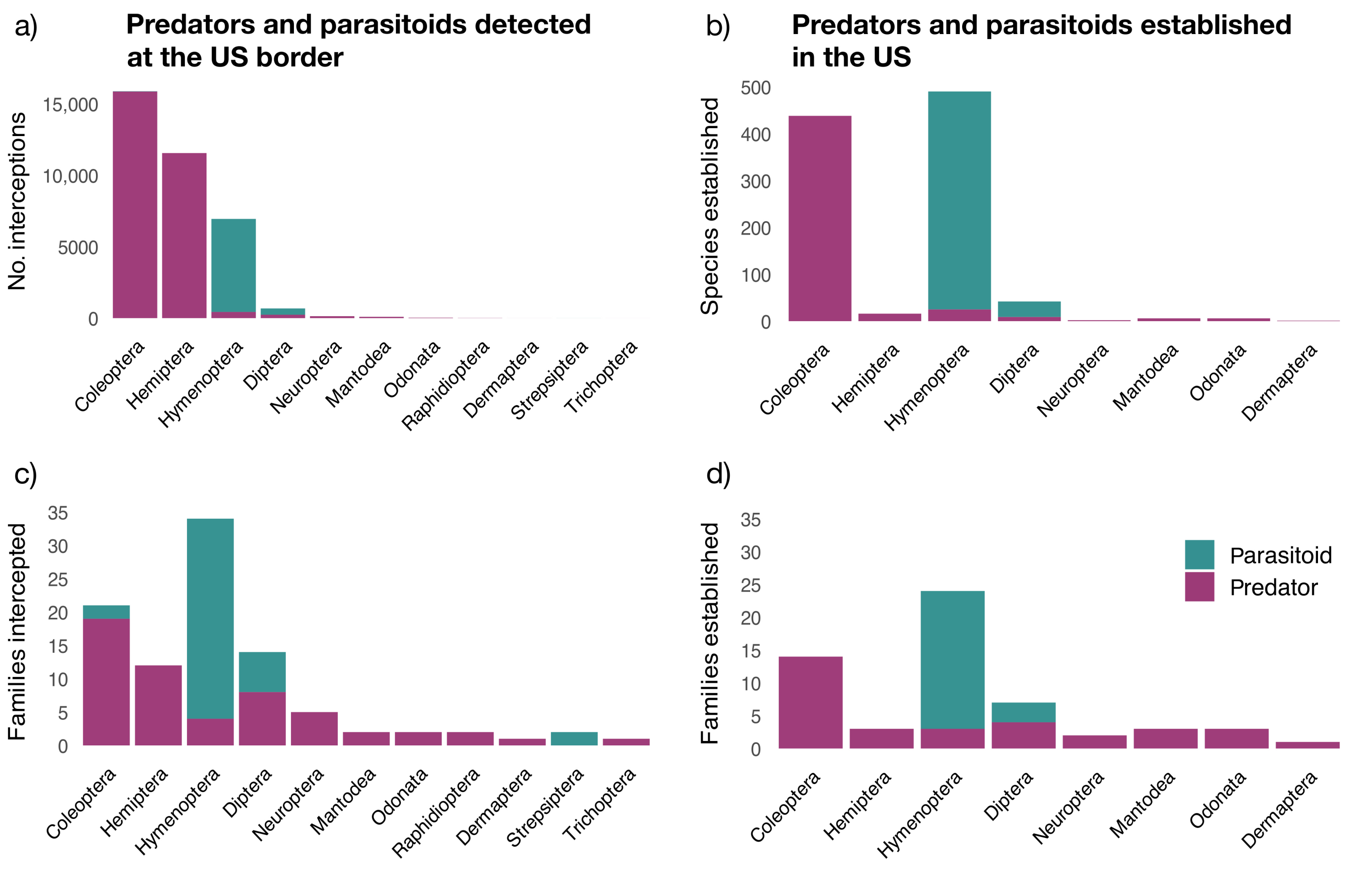

FIGURE 1 Non-native insect parasitoids (pink) and predators (turquoise) by order. (a) The number of interception events, (b) the number of established species, (c) the number of families intercepted, and (d) the number of established families.

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 United States (Figure 1b,d). Within the families we analyzed, 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 United States 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 (Appendix S1: 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.”

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 16 species intercepted 10 or more times with known commodities (Figure 6b). Their d' ranged from 0.14 (most generalist, *Harmonia axyridis*, Coleoptera: Coccinellidae) to 0.67 (*Pseuderimerus indicus*, Hymenoptera: Torymidae). Of these 16 species, 11 were polyphagous. There was no significant association between host specificity and commodity specialization (Kruskal–Wallis $\chi^2 = 3.29$, $p = 0.35$), nor between commodity specialization and whether the species have established in the United States or not (Kruskal–Wallis $\chi^2 = 0.11$, $p = 0.74$). However, the four parasitoid species intercepted 10 or more times were significantly more specialized in their commodity associations than the predator species (Kruskal–Wallis $\chi^2 = 4.25$, $p = 0.03$) (Appendix S1: Figure S2).

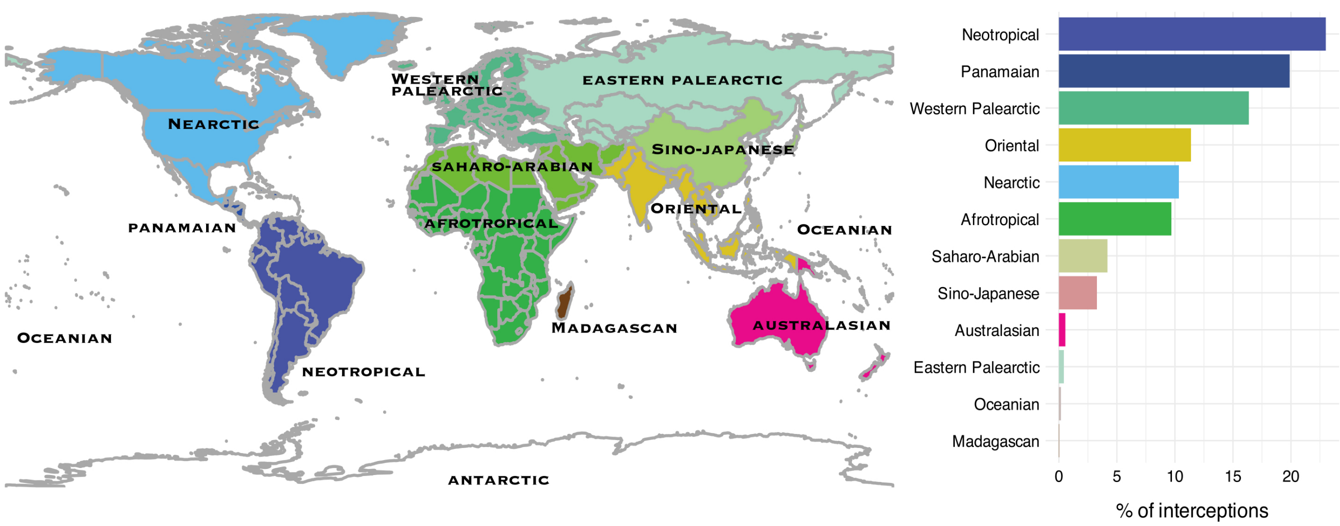

FIGURE 2 The biogeographic regions where commodities transporting insect predators and parasitoids to the United States were imported from, and the percentage of interceptions arriving from each region. Biogeographic regions were delineated based on the distributions and phylogenetic turnover of amphibian, bird, and mammal species (Holt et al., 2013).

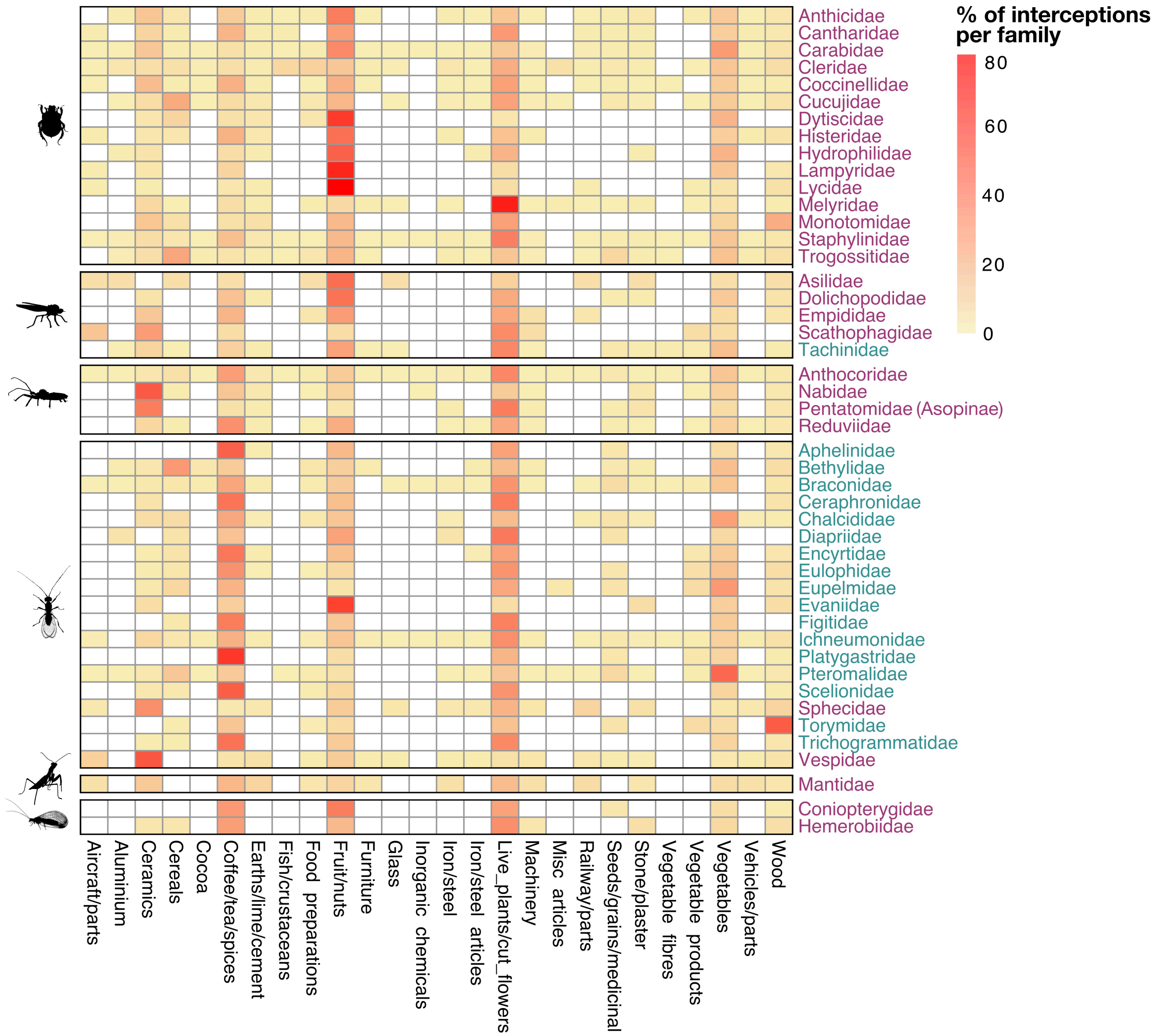

FIGURE 3 Commodity associations of predator (pink) and parasitoid families (turquoise). Only families and HS-2 commodity groups with at least 20 interceptions are plotted. Families are grouped by order: Coleoptera, Diptera, Hemiptera, Hymenoptera, Mantodea, and Neuroptera from top to bottom (image silhouettes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

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 *Ps. indicus* (Hymenoptera: Torymidae) which has *Systole albipennis* (Hymenoptera: Euytomidae) (Poelen et al., 2014) as a known host, *L. sphenophori* (Diptera: Tachinidae) with host *Rhabdoscelus obscurus* (Curculionoidea: Coleoptera) (Leeper, 1974), and *Hexacola neoscatellae* (Hymenoptera: Figitidae) with hosts *Scatella stagnalis* (Diptera: Ephydridae) (Diamond et al., 2001) and *S. tenuicosta* (Castrillo et al., 2008), 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.

Several of the intercepted species have already established in the United States (Figure 8a), either through intentional releases or as unintentional introductions. Other species are considered damaging, that is, 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

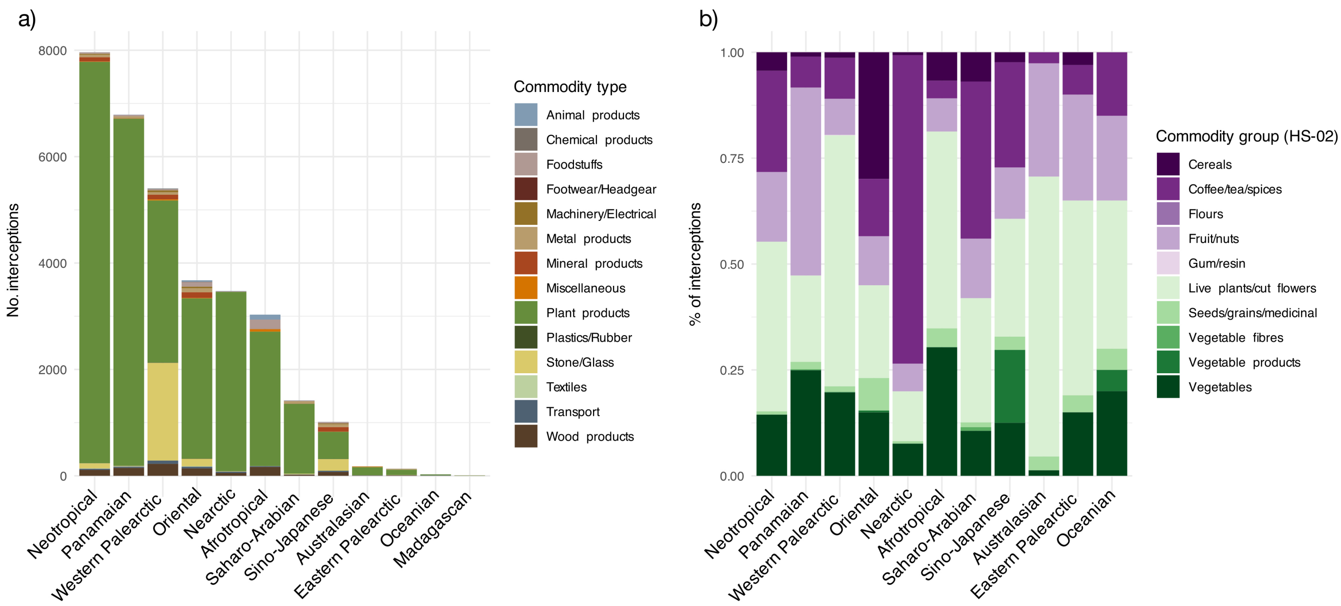

FIGURE 4 Biogeographic region of origin for commodities transporting entomophagous insects. (a) The number of interceptions per commodity class for each region and (b) the percentage of interceptions with commodities classed as "plants and plant products" per region.

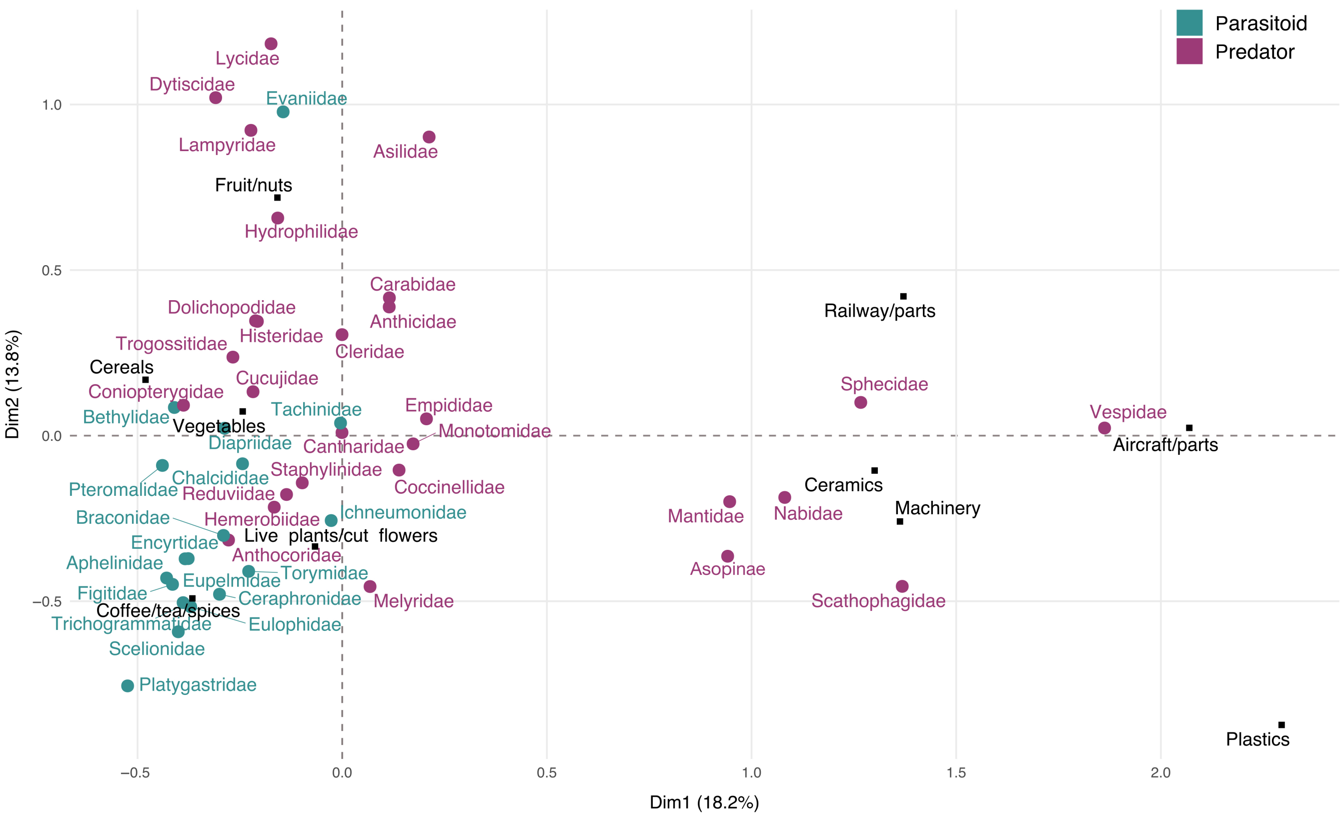

FIGURE 5 Correspondence analysis of commodity associations by family. Predators are shown in pink, parasitoids in turquoise. The 10 HS-2 commodities contributing the most to the ordination are labeled in black.

United States (Figure 8b, *Ropalidia marginata*, *V. vulgaris*, and *Polistes chinensis*, all Vespidae). Of the 196 intercepted species, 50 have been intentionally introduced for biological control either in the United States or elsewhere in the world, and a further 19 species have been studied as potential biological control agents. However, there was no

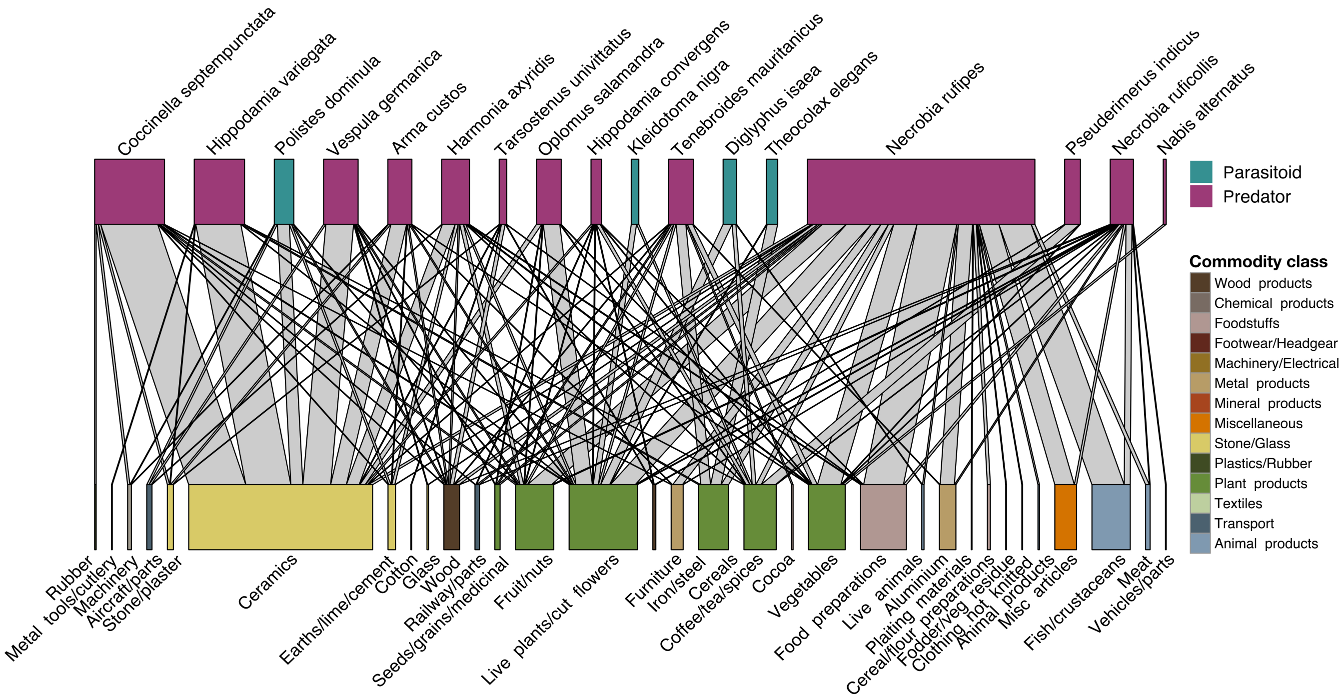

FIGURE 6 Specialization in commodity associations of parasitoid (turquoise) and predator (pink) species intercepted at least 10 times. Commodities are colored by the broad class of product (HS-2 commodity groups) that they were transported with. Commodities are colored by the broad class of product.

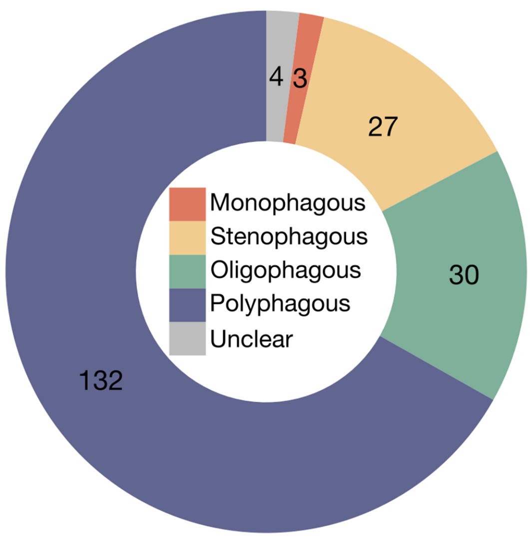

FIGURE 7 Host specificity of intercepted predator and parasitoid species. Species are monophagous (hosts or prey from one genus), stenophagous (hosts or prey from one super-family), oligophagous (hosts or prey from one order), or polyphagous (hosts or prey from multiple orders).

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*, *H. axyridis*, and *Tenodera sinensis*). Of the predator species already established in the United States, 84.3% were generalists (24 polyphagous, 8 oligophagous). We identified at least one known host species present in the United States 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, 88.2% are generalists (90 polyphagous, 15 oligophagous), suggesting that failure to find suitable prey is unlikely to explain their establishment failure.

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

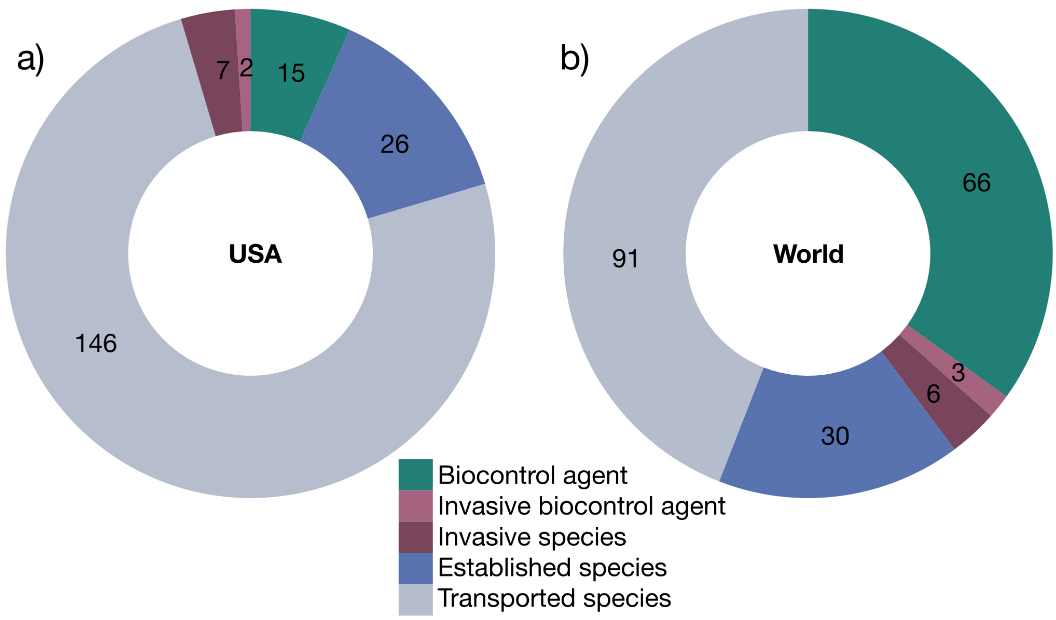

FIGURE 8 Invasion status of intercepted predator and parasitoid species (a) in the United States and (b) globally. Transported species (gray) are not otherwise categorized. Biocontrol agents include both species introduced or studied for biological control. Of 69 world biocontrol species, 47 have successfully established outside of their native range.

established in the United States have known hosts present there.

While the initial arrival and establishment of non-native predators and parasitoids generally go 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 et al., 2011) and 64% of non-native parasitoids in North America (Weber et al., 2021). We found that 93 of the 194 predator or parasitoid families we targeted 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 behavior influence species' probability of entering and surviving human-mediated dispersal, as well as detection during inspections (Gippet et al., 2019; Liebhold et al., 2016; 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 et al., 2018; Turner et al., 2021). Temporal variation in inspection efforts, targets, and species identification may also affect the detection of natural enemy insects (Dowell et al., 2016; 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 underdeveloped 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 United States 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 United States, 37 have already established elsewhere outside of their native range. *V. vulgaris*, *Ropalidia marginata*, and *Po. chinensis* (Hymenoptera: Vespidae) are further listed as invasive and might cause similar damage if they eventually establish in the United States. More positively, 39 intercepted species have been intentionally introduced or studied as potential biocontrol agents internationally, and could potentially also control pests if established in the United States.

The movement of plants and plant products is a well-known pathway for plant pest introductions worldwide (Fenn-Moltu et al., 2022; Liebhold et al., 2012; Meurisse et al., 2019), 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 United States (Fenn-Moltu et al., 2022; Haack, 2011; Work et al., 2005), likely due to extended periods of storage outside providing favorable harborage 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 parasitize 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. Dowell et al. (2016) showed a similar pattern for non-native macroinvertebrates arriving in California. This is likely driven by patterns of historical plant imports to the United States, dominated by Central America and Europe (MacLachlan et al., 2021). The global trade network is continuously evolving, however (He & Deem, 2010). As the sources and types of commodities imported shift, the community of insects arriving will likely follow suit. Insects arriving from regions with a more similar climate and seasonality may be more likely to successfully establish, but fine-scale information on species' native ranges would be required to explore this further.

Biological control agents are often collected in limited numbers from a few sites (DeBach & Rosen, 1991), followed by further loss of genetic diversity due to mortality in transit and inbreeding during mass-rearing (Franks et al., 2011; Woodworth et al., 2002). 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 et al., 2023). Genetic admixture once introduced can further increase standing genetic diversity, create heterosis (hybrid vigor), and potentially enhance species' ability to adapt to new conditions (Kolbe et al., 2008; Müller-Schärer et al., 2023; Szűcs et al., 2012).

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 & Strong, 1996; Snyder & Evans, 2006), and parasitizing 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 (Crowder & Snyder, 2010; Louda et al., 2003). The diet of insect predators is generally less specialized than that of 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., *H. 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 (Leung et al., 2014; Magarey et al., 2009). Improved phytosanitary practices should be associated with pathways that are particularly likely to result in new accidental biocontrol introductions. Additionally, surveillance programs using baited traps for the early detection of non-native insects also collect diverse nontarget species as bycatch (Mas et al., 2023). Identifying these unintentionally trapped species can improve our ability to detect ongoing invasions of entomophagous insects.

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 the establishment of non-native parasitoids and predators can help to detect, avoid, and manage their negative impacts while benefiting from the positive ones.

AUTHOR CONTRIBUTIONS

Andrew M. Liebhold conceived the original idea. Donald C. Weber, Andrew M. Liebhold, and Gyda Fenn-Moltu identified target taxa. Gyda Fenn-Moltu curated and analyzed the data with support from Cleo Bertelsmeier. All authors contributed to the design, discussed the results, and contributed to the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Fenn-Moltu, 2024a) are available in Dryad at https://doi.org/10.5061/dryad.rjdfn2zjj. Code (Fenn-Moltu, 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.8367788.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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