Global Ecology and Biogeography

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Global Ecology and Biogeography

RESEARCH ARTICLE OPEN ACCESS

Border Interceptions Reveal Variable Bridgehead Use in the Global Dispersal of Insects

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Received: 13 September 2023 | **Revised:** 5 September 2024 | **Accepted:** 17 September 2024

Handling Editor: Jonathan Lenoir

Funding: The authors received no specific funding for this work.

Keywords: border interceptions | ecological filters | global invasion | insect invasion | invasive species | phytosantiary

ABSTRACT

Aim: The global, human-mediated dispersal of invasive insects is a major driver of ecosystem change, biodiversity loss, crop damage and other effects. Trade flows and invasive species propagule pressure are correlated, and their relationship is essential for predicting and managing future invasions. Invaders do not disperse exclusively from the species' native range. Instead, the bridgehead effect, where established, non-native populations act as secondary sources of propagule, is recognised as a major driver of global invasion. The resulting pattern of global spread arises from a mixture of global interactions between invasive species, their vectors and, their invaded ranges, which has yet to be fully characterised.

Location: Global.

Time Period: 1997–2020.

Major Taxa Studied: Insects.

Methods: We analysed 319,283 border interception records of 514 insect species from a broad range of taxa from four national-level phytosanitary organisations. We classified interceptions as coming from species native range or from bridgehead countries and examined taxonomic autocorrelation of global movement patterns between species.

Results: While 65% of interceptions originated from bridgehead countries, highlighting the importance of the bridgehead effect across taxa, patterns among individual species were highly variable and taxonomically correlated. Forty per cent of species originated almost exclusively from their native range, 28% almost exclusively from their non-native range and 32% from a mix of source locations. These patterns of global dispersal were geographically widespread, temporally consistent, and taxonomically correlated.

Conclusions: Dispersal exclusively from bridgeheads represents an unrecognised pattern of global insect movement; these patterns emphasise the importance of the bridgehead effect and suggest that bridgeheads provide unique local conditions that allow invaders to proliferate differently than in their native range. We connect these patterns of global dispersal to the conditions during the human driven global dispersal of insects and provide recommendations for modellers and policymakers wishing to control the spread of future invasions.

1 | Introduction

The global, human-mediated dispersal of invasive species from their native to non-native ranges is a major driver of ecosystem conversion, biodiversity loss, crop damage, public health concerns and other effects of global change (Simberloff et al. 2013). The rate of human-mediated accumulation of alien species continues to accelerate (Seebens et al. 2017; Seebens, Bacher, et al. 2020), driven by globalisation and increases in trade, passenger travel and transportation connectivity (Bertelsmeier 2021; Colunga-Garcia and Haack 2015; Hulme 2009; Liebhold et al. 2006; van Kleunen et al. 2015; Work et al. 2005). Insects are among the most damaging animal invaders in terrestrial ecosystems (Bradshaw et al. 2016). Their often-close association with human movements and trade (Faulkner et al. 2020; Hulme 2009), combined with a wide range of life history strategies, means that invasions can rapidly accelerate and become a global problem in just a few years (Campos et al. 2017).

Inspections of incoming containers and vessels at ports of entry for insects are a common tactic of many national biosecurity programs (Saccaggi et al. 2016). Although only a portion of incoming material is usually screened due to the large volume of daily global trade, border interceptions of pests are generally regarded as a proxy for propagule pressure (Turner et al. 2021) that provides insight into how insect species move through the global trade network. The volume of commodity imports influences the rate of species introductions (Levine and D'Antonio 2003), global trade patterns influence the distribution of alien species introductions (Chapman et al. 2017) and interceptions broadly reflect the relative species composition and richness of a source region (Turner et al. 2021). Prior efforts have utilised these associations to make predictions about invasive species transport and establishment (Paini and Yemshanov 2012; Seebens et al. 2016; Seebens, Bacher, et al. 2020).

Border interceptions cover invasive species at varying points in that species' invasion history. Many commonly intercepted pests, such as wheat weevil (*Sitophilus granarius*, Coleoptera: Curculionidae), have been transported by human activity since the dawn of agriculture (Plarre 2013), while others, such as silverleaf whitefly (*Bemisia tabaci*, Hemiptera: Aleyrodidae) (Oliveira, Henneberry, and Anderson 2001), became globally widespread with the arrival of global trade and the industrial revolution. Other intercepted species, like the red imported fire ant (*Solenopsis invicta*, Hymenoptera: Formicidae) (Ascunce et al. 2011), or the tomato leafminer (Tuta *absoluta*, Lepidoptera: Gelechiidae) (Campos et al. 2017), are in the early or middle stages of global invasion with ranges that are still expanding. A majority of intercepted species are infrequently detected (Turner et al. 2021), and some of these species may be interpreted as incidental hitchhikers in commodity shipments, transported on materials that are not their host plants. However, many of these infrequently intercepted pests represent contaminants that may become damaging future invaders, and predicting which species pose the greatest risk is an ongoing area of study (Turner et al. 2020).

Blackburn et al. (2011) defined four stages for the progression of a biological invasion: transport, introduction, establishment and spread, each of which acts as an ecological filter, selecting for species or phenotypes that are able to succeed at all phases of the invasion process (Clobert et al. 2009; Renault et al. 2018; Ronce 2007). Gippet et al. (2019) specifically adapted the concept of invasion phases and their inherent ecological filters to the global, human-driven dispersal of insects, defining departure, transport and establishment as the three relevant stages. This modified framework provides important specificity in the transport stage that is relevant to the discussion of insect invasion examined through interception data because interception data only directly provides information about contamination success—information about survival during transport and later establishment can only be inferred from successful future invasions using interception data.

Conceptual models of global insect invasion (Hellmann et al. 2008; Peacock and Worner 2006) typically focus on flow from species' native ranges as sources, to introduced ranges as sinks. Intermediate, non-native populations (termed 'bridgeheads') are increasingly recognised as a source of new species introductions and as a possible inflection point for rapid behavioural and morphological change, which can alter the trajectory of an ongoing global invasion (Bertelsmeier and Keller 2018; Bertelsmeier and Ollier 2021; Lombaert et al. 2010).

Bertelsmeier et al. (2018) found that 75%–87% of ants intercepted at points of entry into the United States and New Zealand originated from bridgehead locations outside their native range, indicating that for some taxa, bridgeheads can be a significant driver of future invasions. However, ants possess complex social structures and can completely reform the environments they invade (Holway et al. 2002), thus global dispersal patterns in ants may not be representative of other invasive insect taxa. A number of other works have drawn attention to the role of the bridgehead effect in accelerating global invasions in a variety of taxa including termites (Blumenfeld et al. 2021; Blumenfeld and Vargo 2020), a moth (Bras et al. 2022), a mealybug (Correa et al. 2019) and a seed bug (Lesieur et al. 2019). However, there is still a lack of comparative studies that quantify the role of the bridgehead effect on propagule pressure across diverse insect taxa. A full understanding of how bridgeheads accelerate the global dispersal of invaders and whether all invasive insect taxa uniformly utilise bridgeheads is still a critical knowledge gap for understanding the global dispersal of insects.

Our objective is to better understand the role of bridgeheads in the global-scale spatial spread of insects. We quantify the amount of global propagule pressure originating in species native or non-native ranges in order to assess if (1) bridgeheads play a similar role in driving global propagule pressure for all insect species (versus ants and other selected species) and (2) patterns of propagule pressure are consistent between individual species. To our knowledge, our dataset is the largest, multi-family dataset combining interceptions with native range data. We hypothesise that many taxa will only be intercepted in shipments originating from their native range, representing a sampling of the fauna present in origin countries, whereas species that experienced human-mediated range expansion in historical times or are in the midst of current global range expansion should originate from a mixture of source locations, that is, that approximately 75%–87% (Bertelsmeier et al. 2018) of interceptions originate from invaded locations.

2 | Methods

We analysed records of insects intercepted in vehicles and commodity shipments of air, land and sea cargo and mail at ports of entry in the United States (USDA APHIS 2019), the European Union (EUROPHYT 2021), Japan (MAAF 2021) and South Africa (Saccaggi et al. 2021) during 1997–2020 (details available in Supporting Information—Worm et al. 2024). Interception records used in this study contain information on the intercepted pest, date of interception and the origin location of the intercepted commodity (i.e., the location where the contaminated goods were grown or packed, rather than the last leg of the goods' journey), as determined by the intercepting agent or agency. Interceptions from the United States excluded records for non-reportable pests, which generally include species that have long been established in the United States and are widely distributed there. We excluded interceptions of insects on passenger baggage because the origin location of the passenger's journey was not consistently recorded. The number of individual organisms intercepted in a shipment is not recorded and thus one interception record represents the interception of one or more individuals of a species. This recording scheme makes it challenging to draw inferences about propagule pressure from specific commodity pathways but allows comparison of the biological diversity of intercepted organisms.

The level of taxonomic detail reported (i.e., naming standards followed, reporting at the genus level and above) is variable between intercepting countries and individual records. We excluded all interceptions not identified to the species level. Raw taxonomic information also contained misspellings, outdated taxonomy or informal nomenclatural designations of uncertainty (e.g., *f.*, *cf.*). To standardise taxonomy across sources, we adapted the taxonomic standardisation methods detailed by Turner et al. (2020). Using R packages taxize (Chamberlain et al. 2020; Chamberlain and Szocs 2013) and rgbif (Chamberlain et al. 2022), we matched raw names to standardised names provided by the Global Biodiversity Information Facility (GBIF 2021) (GBIF) taxonomic backbone. Names that did not match GBIF taxonomy were additionally compared to 10 other taxonomic backbone providers including the Catalogue of Life Checklist, National Center for Biotechnology Information (NCBI) and Encyclopedia of Life (complete list available in Supporting Information). Although it was infeasible to manually check all corrected names, comparisons of raw and corrected names showed a high degree of accuracy. Raw names of exporting countries similarly exhibited misspellings and inconsistencies, which we standardised to ISO-standard 3-letter abbreviations using Python package country converter (Stadler 2017).

Native-range information for intercepted species was acquired from a combination of data from the Delivering Alien Invasive Species Inventories for Europe (DAISIE) checklists formerly Research Institute for Nature and Forest (INBO) and the Centre for Ecology and Hydrology (CEH), now hosted by GBIF (GBIF 2021; Hulme et al. 2010), unpublished data from Yu Takeuchi and manual entry from published literature (available in Supporting Information (Worm et al. 2024)). When native range information was unavailable from other sources, we manually searched published literature for each species, in descending order of the number of interceptions. We determined an effort threshold in our manual literature search of 25 consecutive species with no published native range information, resulting in a search conducted for all species with more than 30 interceptions. The remaining species with fewer than 30 interceptions and no native-range information from the previously mentioned datasets comprise 3% of total interception records.

Geonyms provided for species' native ranges were variable, including countries, biogeographic zones, continent names and mountain ranges. All geographic designations were recoded using a crosswalk (provided in Supporting Information (Worm et al. 2024)) to one or more of the biogeographic zones containing the listed native range from the set of the Western Palearctic, Eastern Palearctic, Neartic, Neotropical, Afrotropical, Australasian and Oriental regions (e.g., 'Carpathian Mountains' became 'Eastern Palearctic' and 'Tasmania' became 'Australasia'). We initially investigated the differences between the determined source region of intercepted species based on the level of geographic aggregation (assigning native ranges as biogeographic zones, geographic continents or United Nations–designated subregions) but found minimal differences (2%–5%) in the overall proportion of interceptions so opted to use biogeographic zones exclusively. A crosswalk of countries and their containing biogeographic zones was obtained from AntWiki (*Countries by Regions—AntWiki*, n.d.) and modified to include multiple biogeographic zones for large countries spanning multiple bioregions (United States, Mexico, China, Russia). Because of a large number of native range records that specified Europe or Temperate Asia, we split the Palearctic into Eastern and Western zones. A complete list of country/bioregion assignments is available in the Supporting Information.

Intercepted species were considered as coming from their native range if the recorded native range of the pest included the origin country of the interception, and as coming from a bridgehead location if the origin country was outside the species' native range. The interception data we utilised records the origin location of the intercepted commodity (i.e., where the goods originated and were packed) to the best estimate of the intercepting agency. It is possible that some interception records are erroneous because they came from shipments with falsified information, containers that become contaminated in transit (e.g., while sitting at the dock in an intermediate port) or containers that were insufficiently cleaned and contained contaminant organisms from a previous shipment, though we consider these scenarios to be uncommon and unlikely to impact the results of our analysis. Species with a cosmopolitan or otherwise unknown native origin were excluded from native range analysis. For each species, we evaluated the portion of interceptions originating in native versus bridgehead locations (interceptions from bridgeheads/total interceptions), which we refer to as the 'bridgehead proportion'.

To examine patterns of global invasion between related species, we calculated phylogenetic autocorrelation of the bridgehead proportion between all intercepted species with at least 100 interceptions (Figure 1, $n = 308$) with Moran's I, a commonly used measure of spatial autocorrelation. Instead of calculating autocorrelation over spatial distance, we calculated autocorrelation over phylogenetic distance using the phylocorrelogram function in R package phylosignal (Keck et al. 2016). Because publicly available genetic data to calculate phylogenetic distances were unavailable for approximately two-thirds of the species in our dataset, we utilised taxonomic relationships with a uniform weighting (0.1 per taxonomic rank) as a stand-in for phylogenetic distance, as utilised by Oden and Sokal (1986), with the understanding that current taxonomy may not always perfectly reflect phylogeny.

To confirm that interceptions recorded as coming from bridgeheads represent likely established populations and not records of en-route contamination, we combined invasive insect occurrence records from the CAB International Invasive Species Compendium (CABI 2021), the European and Mediterranean Plant Protection Organization Global Database (EPPO 2022), the Standardising and Integrating Alien Species dataset (SInAS) (Seebens 2021; Seebens, Clarke, et al. 2020), GBIF occurrence and DAISIE (Hulme et al. 2010). Because these datasets, with the exception of GBIF, primarily document non-native populations, we considered any interception from a native-range country to be legitimate and not a result of contamination, though this assumption could potentially slightly underestimate the proportion of interceptions originating in bridgeheads. Methodology for harmonising occurrence records modified from Saffer et al. (2024). Further details on occurrence records are also provided in the Supporting Information (Worm et al. 2024).

To further confirm interception patterns of species intercepted exclusively from their native range (hereafter All-Native species) arose from differences in distribution rather than selection through pathways (i.e., evidence that All-Native species show fewer establishments despite high propagule pressure), we performed an additional literature search for the top 20 most frequently intercepted All-Native species (references by species available in Supporting Information (Worm et al. 2024)).

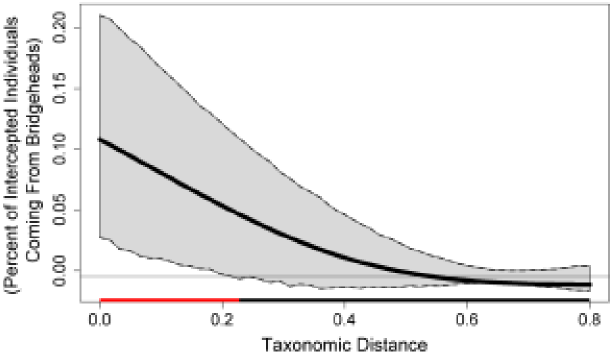

FIGURE 1 | Taxonomic autocorrelation (Moran's I) of bridgehead proportion among all taxa with > 100 interceptions ($n = 207$). Taxonomic weighting was applied evenly across taxonomic levels (distance of 0.1 per level). Statistically significant autocorrelation up to phylogenetic distance 0.2 represents autocorrelation at the genus and (to a lesser degree) family levels. Shaded area represents 95% confidence interval from 2500 bootstrap replicates.

3 | Results

During the period from 1997 to 2020, there were 369,754 interceptions representing 4852 insect species at points of entry in the United States, the European Union, Japan and South Africa. From these, interception records for 514 species with species-level taxonomy and native information were kept for further analysis, comprising 319,283 (Table 1) or 86% of interceptions. Cosmopolitan species (i.e., species with a global native range) make up a substantial portion of the unused records—the 10 most frequently intercepted cosmopolitan species account for 51% of the unused records. Species with more than 30 interceptions for which native range information was unpublished or could not be found comprise 34% of records without native range information (5% of total records). Species with fewer than 30 interceptions comprise the remaining 15% of records without native range information, or 2% of total records. In total, 7% of all interception records were lacking native range information and 7% of records were cosmopolitan species excluded from further analysis.

The distribution of interceptions per species is approximately power-law distributed ($p = 0.51$ versus null model of non-power-law distribution, 100 bootstrap replicates using R package poweRlaw (Gillespie 2015)) (Figure 2A), with the most commonly intercepted species being *Dysmicoccus neobrevipes* (Hemiptera: Pseudococcidae; 30,093), *Dysmicoccus brevipes* (Hemiptera: Pseudococcidae; 21,544), *Lepidosaphes beckii* (Hemiptera: Diaspididae; 21,190) and onion thrips, *Thrips tabaci* (Thysanoptera: Thripidae;19,746). The median number of interceptions per species was 395. The top 10% of species by interception number represent approximately 80% of the total identified interceptions with native range information. Many of the most-commonly intercepted species include common agricultural pests that utilise piercing/sucking feeding (Thrips, scale insects) and frequently reach high population densities in affected areas. Though intercepting countries show variation in the exact species imported, overall proportions of species orders are loosely comparable between destination countries, though there is considerable intercountry variation (Figure 3).

For the 514 species used in our analysis, 65% of interceptions originated from bridgehead regions, that is, outside of the native

TABLE 1 | Identified interception volume by intercepting country.

Country	Number of identified interceptions (with species-level taxonomy + native range information)	Number of intercepted species
United States	54,848	243
South Africa	657	101
Japan	251,904	321
European Union	26,550	125

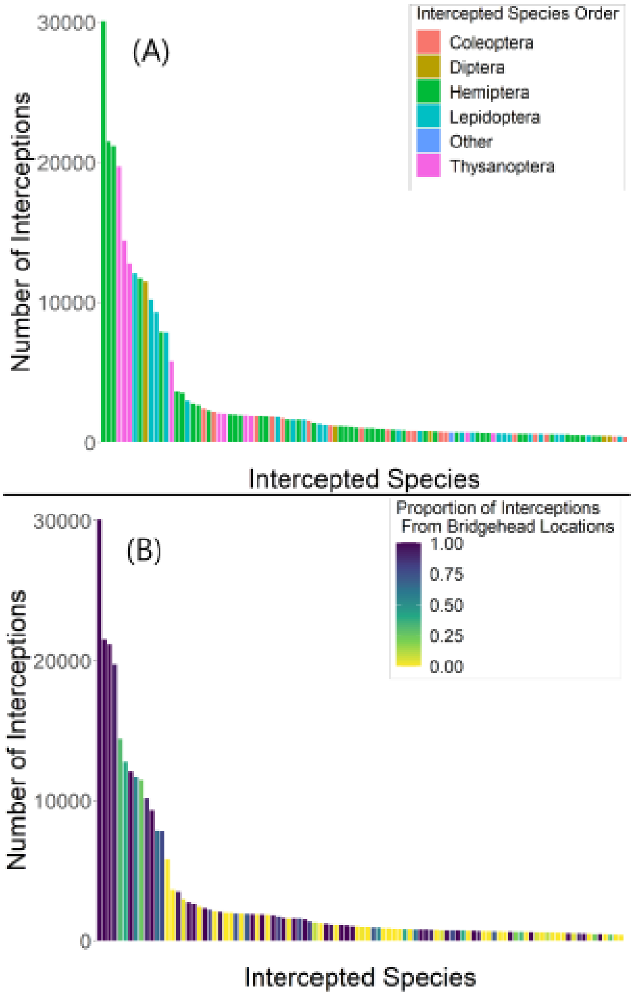

FIGURE 2 | Top 100 most frequently intercepted species, 1997–2020. Species interception frequencies are approximately power-law distributed. Interceptions are coloured by order in (A) and bridgehead proportion (B).

range of the intercepted pest. Due to the high number of interceptions of a small number of widely invasive species that were almost exclusively intercepted from bridgeheads, the proportion of origin locations for all interceptions skews towards bridgeheads. The top four most frequently intercepted species in our dataset were intercepted exclusively coming from their non-native range. Species with fewer than 30 interceptions each display an average bridgehead proportion of 58%.

Ninety per cent of analysed records were intercepted from countries with a recorded presence of the intercepted species. 85% of interceptions from non-native locations had recorded occurrence records and all native-range interceptions were considered recorded presences if the species was native to the bioregion of the origin country of that interception. If only interceptions with a recorded species presence in the origin country are used (90% of records), the overall percentage of interceptions from bridgeheads is 61.4%.

If all intercepted and identified species lacking native range information were intercepted from shipments originating in the native range, the overall proportion of bridgehead interceptions would drop to 60%. If all species lacking native range information were intercepted from non-native regions, the total proportion of bridgehead interceptions would be 68%. In other words, there is a maximum (though highly unlikely) uncertainty attributed to unidentified species of +3%/−4.6% on our estimate of 65% of interceptions originating in bridgeheads. If the true bridgehead proportion of species lacking native range information were 50% (which is considerably lower than our observed bridgehead proportion), uncertainty on our estimate of the proportion of bridgehead interceptions is ±1%.

There was no strong geographic pattern between the origin location and bridgehead proportion (i.e., the percentage of interceptions of a given species originating in bridgeheads) of interceptions (Figure 4), with countries of varying size, location and economic ability exporting varied mixtures of native and non-native species. Notably, Brazil, a country known for its high native biodiversity, exported almost exclusively non-native species.

The origins of interceptions in aggregate highlight the prominent role played by bridgehead regions in promoting the global dispersal of insect species. However, the interception records of individual species describe distinct patterns in their global dispersal. We considered all species with more than 100 interceptions (204 species) to be robustly sampled enough to determine species-level patterns of interception. The dispersal patterns of individual species show significant taxonomic correlation within genera and to a lesser degree within families (Figures 5, 6). In this pool of frequently intercepted species, 40% of species ($n=81$) were intercepted almost exclusively (>95%) from their native range, 29% ($n=63$) were intercepted almost exclusively (>95%) from their non-native range and 31% ($n=58$) were intercepted from a mixture of their native and non-native range (Figure 7). Seven of the 15 most frequently intercepted species were intercepted exclusively from their non-native range, 2 of the 15 exclusively from their native range and 6 of the top 15 from a mix of native and non-native source regions. We term these dispersal patterns as 'All-Bridgehead', 'All-Native' and 'Mixed-Range', respectively, and further report their characteristics below.

Mean interannual standard deviation for the bridgehead proportion of species intercepted more than 100 times was 0.10 with a coefficient of variation of 0.73 and the absolute average linear slope across the study period (change in bridgehead proportion/year for a given species) was 0.007.

Of the top 20 most-intercepted All-Native species, (total 37,796 interceptions, average 1890 interceptions per species), 15 species had never been recorded from a non-native country (occurrence records collected from literature and databases of species occurrence, detailed in Supporting Information—Worm et al. 2024). *Thaumatotibia leucotreta* (Lepidoptera: Tortricidae) and *Diabrotica undecimpunctata* (Coleoptera: Chrysomelidae) were recorded from a single non-native country, *Earias vittella* (Lepidoptera: Nolidae) from two non-native countries and *Amrasca biguttula* (Hemiptera: Cicadellidae) and *Spodoptera litura* (Lepidoptera: Noctuidae) from 3 to 4 non-native countries, although some presence records were dubious. On average, the top 20 All-Native species were intercepted from 10.9 origin countries each, suggesting that their All-Native interception pattern is not likely to be caused by a high propagule pressure from a single origin country.

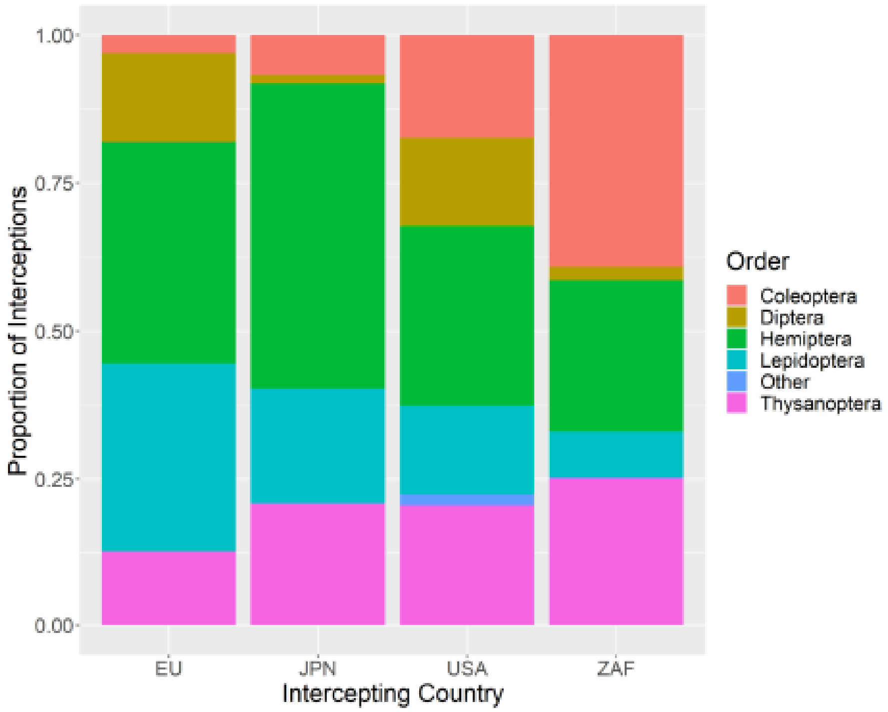

FIGURE 3 | Relative proportions of intercepted orders for all intercepted species identified to the species level, by intercepting country. All countries show roughly comparable ratios of intercepted orders. Some local differences may be attributable to the amount of taxonomic attention applied to particular groups as well as the hyper-abundance of individual species.

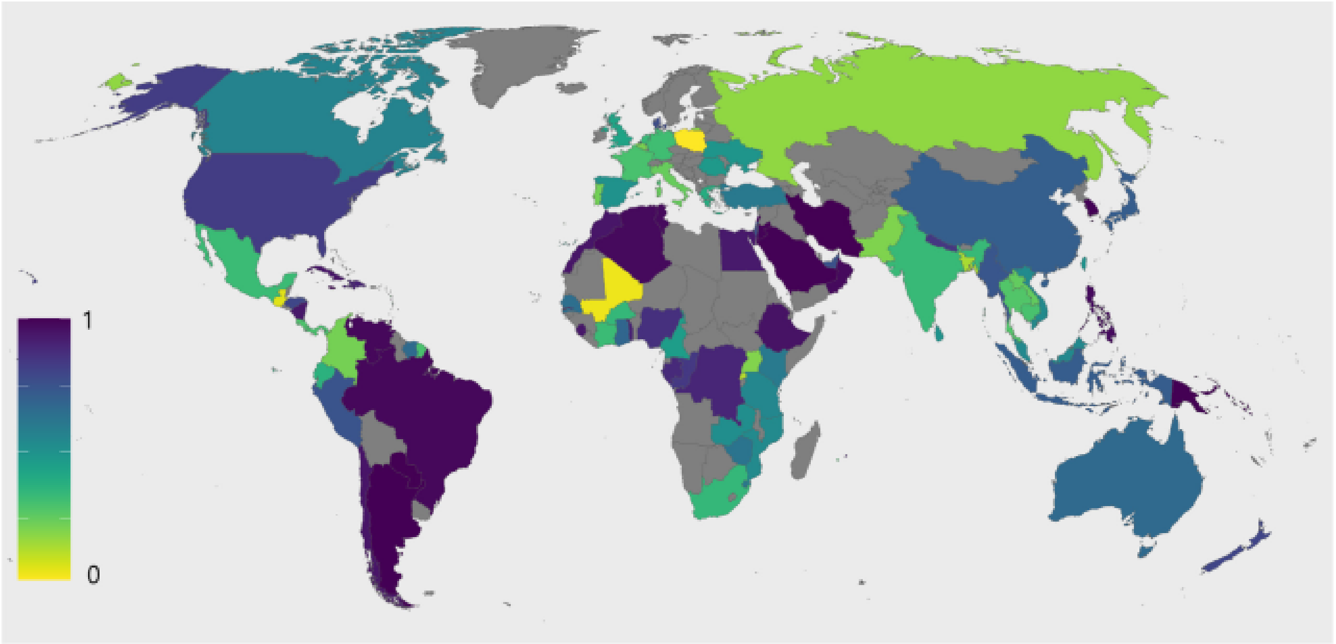

FIGURE 4 | World map, countries that originated > 100 interceptions. Colour denotes the bridgehead proportion of interceptions originating in that country. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

4 | Discussion

Our observed proportion of interceptions originating in bridgehead regions (65%) is slightly lower than the estimates of 75%–87% obtained by Bertelsmeier et al. (2018). Their focus on a single family with data beginning in 1914 through 2013 (1914–1984 in the United States, 1955–2013 in New Zealand) presents an excellent picture of the global dispersal trends in ants over

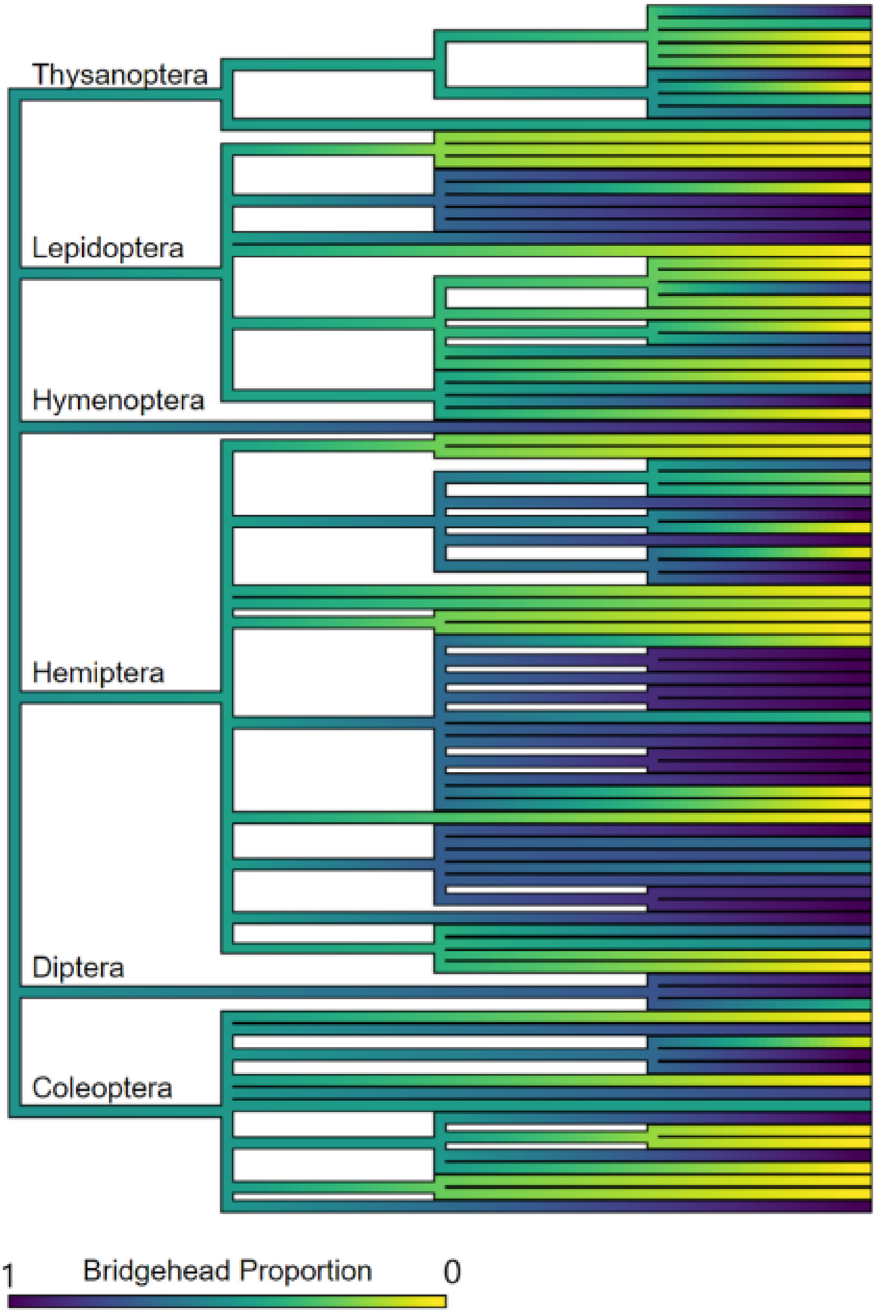

FIGURE 5 | Bridgehead proportion for the 100 most frequently intercepted species. Branch tips (right) represent individual species, and lower nodes represent genera, families, etc. A limited sample of all intercepted species is shown for illustrative purposes, though patterns of taxonomic clustering within genera and families are apparent. Figure 1 shows statistical metrics of bridgehead proportion clustering.

the last century, but may not accurately represent trends in the global dispersal of all insect taxa in the era of containerised shipping and modern globalisation.

Interception data present an imperfect understanding of global insect flows because many intercepted species are never fully identified (as evidenced by the many thousands of records we received identified only to genus or family). Infrequently intercepted species may be less likely to receive species-level taxonomic designation from the intercepting phytosanitary agency because of their taxonomic obscurity, given that 80% of insect species have yet to be described (Stork 2018), and thus are excluded from further study. Although information on the specific biases in interception data are unavailable, interceptions may preferentially select pest species that are familiar to inspectors, pests that are more visible on traded goods, or commodities often containing pests that are consciously or unconsciously inspected at a higher rate. Thus, while our discussion applies generally to the global flow of insects to the best of our knowledge, it may be more relevant to insects that are considered pests as a result of their close association with human activities.

Bridgeheads play a disproportionately large role in accelerating the spread of certain species, particularly so for the most

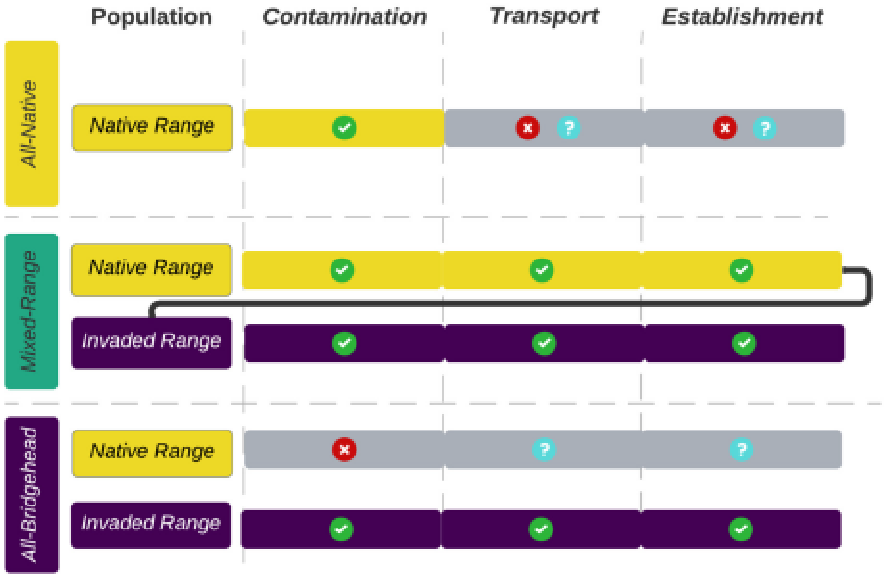

FIGURE 6 | Conceptual diagram of the relationship between observed dispersal patterns and the phases of human-mediated dispersal. All-Native species succeed at contamination leaving their native range, but fail at surviving during transport or establishment (though our data prevent knowing which stage). These failures are likely related directly to species biology. Mixed-Range species succeed at all phases of invasion from both their native and non-native ranges. All-Bridgehead species typically fail at contamination from their native range (except for the rare events that initially establish a bridgehead), but generally succeed at all phases of invasion from their invaded range. In some rare cases, species may be categorised as All-Bridgehead because there are no pathways between the species native range and the intercepting destination countries, though we consider these circumstances to be rare.

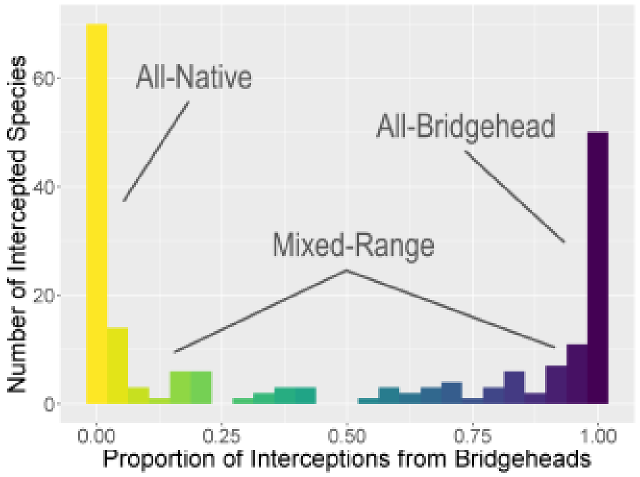

FIGURE 7 | Number of species intercepted, binned by the bridgehead proportion of each species.

commonly intercepted species in our data (Figure 2B). Although a high proportion of bridgehead interceptions is to be expected for widely distributed, globally invasive species with a close association with agriculture, we consider the exclusive bridgehead origin of these species to be significant and noteworthy. However, the bridgehead effect may not be a universally strong driver of all global insect invasions. Even within the top 15-most frequently intercepted species, six were intercepted from a roughly even mix of origins and two from exclusively native regions.

Our data reveal that the bridgehead proportion of intercepted insect species varies, with some species exclusively intercepted coming from their native range (All-Native), some exclusively from bridgehead locations (All-Bridgehead), and some from a mix of native and bridgehead locations (Mixed-Range) (Figure 7). These interception patterns within species are temporally consistent (occurring consistently over decades for many species as shown by consistent annual rates of bridgehead interception), taxonomically correlated (occurring similarly among closely related species) and geographically widespread (occurring from many different countries for each species). We interpret these patterns as evidence that globally spreading insects can display dispersal patterns that differ based on the locations from which they are dispersing—in other words, that some species may not disperse equally well or equally often from their native and non-native ranges and thus that propagule pressure from native and non-native sources may differ by location. There is little obvious spatial pattern to the native or non-native status of exported species (Figure 4)—presumably the observed relationships are driven by a complex mix of species biology, exports, climate, phytosanitary compliance and other factors.

Autocorrelation in the bridgehead proportion within genera and to a lesser degree within families suggests that patterns of human-driven dispersal are at least partially derived from the biological traits shared with other, closely related, intercepted species. Identifying specific traits that facilitate invasiveness has been a goal for researchers (Baker 1974), though even identifying traits in plants is difficult (Barwell et al. 2021; Hulme and Bernard-Verdier 2018; Pyšek and Richardson 2007) and invasive traits in insects have received considerably less attention, likely due to the complexity of insect behaviour (e.g., diapause in many different life stages, host plant relationships, mobility). Further, the traits that facilitate global anthropogenic dispersal in insects may only be identifiable during human-driven dispersal, because the unique conditions present during contamination, transport and dispersal differ from typical environmental conditions. Even if the specific traits causing this observed global dispersal pattern are unidentifiable, the knowledge that bridgeheads unequally contribute to global propagule pressure for some groups of species offers important information to assist management decisions.

4.1 | All-Native Species

All-Native species can be conceptually divided into two groups based on their relative number of interceptions. The first group comprises infrequently intercepted species with a handful or several dozen interceptions. This group presumably includes some of the intercepted species for which we could not find native ranges and some species which could not be accurately identified by the intercepting organisation. These species display low propagule pressure, making their future establishment success difficult to predict. While some members of this group could become damaging global invaders, others likely represent incidental hitchhikers or contaminants on commodity shipments with limited invasive potential because of their dependence on a particular host plant or other niche.

The second group of All-Native species have been regularly intercepted hundreds or thousands of times, indicating very high propagule pressure. The high number of interceptions suggests these species display high population densities in human-influenced environments (as agricultural pests or common environmental generalists) and thus could be likely invaders, if provided suitable establishment conditions. The 20 most frequently intercepted All-Native species include *Chaetocnema tibialis* (Coleoptera: Chrysomelidae), *Earias vitella* (Lepidoptera: Nolidae), *Abgrallaspis aguacatae* (Hemiptera: Diaspididae)—all common pests in their native range that specialise on a narrow range of host crops, which lends support to the idea that specialist species have more difficulty establishing in new locations compared to generalists (Malacrida et al. 2007). Among this group of 20 frequently intercepted species, 75% of species have no records of invasion or establishment outside their native range, and the remaining species have invaded 1–4 countries, often in localised areas within the invaded country. Species that are frequently intercepted (implying high propagule pressure) but lack invasion histories apparently lack the ability to readily establish outside their native range and may face ecological filters to their invasion success during transport or establishment (Figure 6).

The processes of global transport and establishment in global transport pathways represent a novel environment for contaminant insects and All-Native species apparently consistently fail at either the transport or establishment phases of dispersal (or both), despite frequent success contaminating shipments during departure (Figure 6). Depending on the pathway, contaminating individuals may spend days or weeks in containers that are refrigerated, hot, dry or otherwise environmentally inhospitable and upon arrival may find themselves in areas with different climatic conditions and host plants than the native range they departed. For species with short generations, limited cold tolerance, a monophagous diet, seasonal life cycles or other needs, the conditions during transport or the environment in their potential new range may prove a substantial barrier. While some portion of the described All-Native species may be successfully established but cryptic outside their native range (Bebber et al. 2019; Crooks 2005), the majority have likely not yet established in bridgehead regions and represent an important mode of global insect movement.

4.2 | Mixed-Range Species

Mixed-Range species display an interception pattern consistent with typical assumptions about global invasive species movement—that invasive species tend to occupy a bridgehead before spreading to the rest of the world from a mixture of native range and bridgehead locations, thereby leading to global invasion. Many of the species displaying this dispersal pattern are well-known global invaders, including *Liriomyza huidobrensis* (Diptera: Agromyzidae, Pea Leaf Miner) and *Helicoverpa armigera* (Lepidoptera: Noctuidae, Cotton Bollworm).

Species displaying this pattern of movement regularly contaminate shipments in both their native and invaded ranges, implying that populations in both ranges may display similar densities and characteristics. It should be re-emphasised that our category of 'Mixed-Range' encompasses species intercepted from 5% to 95% from their non-native range. At the high end, species may be widely globally invasive with propagule primarily coming from previously invaded bridgeheads while at the low end, bridgeheads represent a relatively insignificant proportion of propagule pressure.

4.3 | All-Bridgehead Species

All-Bridgehead species display an interception pattern that breaks from the common assumption that global, human-driven dispersal of invasive insects occurs primarily or in part from the species' native ranges. The relatively high number of origin countries (mean 18, median 13) recorded for individual All-Bridgehead species implies that bridgehead populations of these species are successful contaminators and contribute propagule into the global trade network even while their native ranges are unrepresented as a source of propagule. The apparent gap between success in dispersal from bridgeheads and failure at native range contamination and dispersal in this group of species raises many questions about the spatial patterns of global, human driven insect movement and strongly suggests that for many species, dispersal is influenced by the native or non-native status of the dispersing location.

Although some species could show in our data as All-Bridgehead species because they lack pathways between native range and destination countries, many of the most frequently intercepted All-Bridgehead species in our dataset are associated with cut flowers and fresh produce, which are widely globally traded and unlikely to lack pathways from entire biogeographic zones to any of the four geographically diverse destination locations.

Using the conceptual framework Gippet et al. (2019), native populations of All-Bridgehead species are generally unsuccessful at contamination while bridgehead populations of the species are consistently successful at all three stages (Figure 6). Species may frequently fail at regularly dispersing from their native range because they have limited native ranges or live far from outgoing cargo, because of low population densities, because they natively do not associate with traded commodity species or because they lack traits that facilitate their contamination of outgoing commodities.

Higher densities of invasive species in non-native regions compared to native regions are a commonly reported phenomenon for many species because of enemy release (Colautti et al. 2004), novel weapons (Callaway and Ridenour 2004), eco-evolutionary experience (Saul, Jeschke, and Heger 2013) or other mechanisms. These high densities in non-native regions are a likely driver of the observed differences in propagule pressure between native and non-native regions for All-Bridgehead species. The correlation of bridgehead proportion between related taxa suggests that there may be certain shared traits that facilitate differing abundance in bridgeheads compared to native regions.

A change in contamination from bridgeheads could also be caused by behavioural changes in the species after arrival. Genetic studies comparing native-range populations to bridgehead populations in a planthopper (Du et al. 2021) and a longhorned beetle (Javal et al. 2019) have provided evidence that certain phenotypes or traits may be selected for and accentuated by the process of global invasion. Adaptive evolution, where invasive species accumulate traits that further their invasiveness in bridgehead locations has mixed empirical support (Bertelsmeier and Keller 2018; Prentis et al. 2008; Robinet and Liebhold 2009; Whitney and Gabler 2008), though post-invasion changes in host plant preference (Hsiao 1978; Thomas 1993; Wu et al. 2019) has been long documented and could potentially give rise to our observed pattern of All-Bridgehead interception through a switch to plants with a greater association with traded commodities in bridgehead regions.

4.4 | Limitations

Native range data were unavailable for 7% of the taxonomically identified interceptions in our dataset, leading to slight uncertainty in the overall proportion of global propagule pressure attributable to bridgehead regions. Although theoretical maximum uncertainty is +3/−5%, a more probable estimate of origin of global propagule pressure provides ±1% error on our estimate of 65% of interceptions from bridgeheads. Considerable gaps in the publication and databasing of native range information make it difficult to answer questions about species diversity and origins of global insect propagule pressure, even if overall trends in propagule pressure origin are quantifiable.

The accuracy of origin location in interception records also presents a potential limitation to our work. Although the intercepting agencies in each country make the best attempt possible to estimate the origin location of intercepted goods (see Notes on Interceptions in Supporting Information—Worm et al. 2024), the potential for falsified records and en-route contamination exists and should be noted. We were able to verify the presence of intercepted species in 90% of interception records, resulting in a potential maximum error of −3.5% of overall propagule pressure origin. However, considerable gaps exist in presence records for invasive insects, with as many as 300 unreported species estimated present in some countries (Bebber et al. 2019) It is very unlikely that all unverified presences represent en-route contamination or erroneous records rather than currently un-recorded species presences. This work highlights the need for comprehensive and current global invasive species inventories to facilitate the study of global invasions.

5 | Conclusions

The considerable number of All-Bridgehead species in our data suggest that, for some species, bridgeheads play an outsized role in driving future invasion beyond just their contribution of additional invasion origins. For these species, bridgehead establishment represents a dramatically increased regime of propagule pressure, shifting species from occasional contaminants on commodities to a regular phytosanitary risk. Our data suggest that the bridgehead or native status of an exporting country can have a substantial effect on outgoing propagule pressure and also implies differences in invasion success based on source location. If bridgeheads uniquely shape invasions beyond acting as an additional source of propagule (e.g., through higher population densities in bridgeheads or by inducing genetic change), bridgehead populations may pose an enhanced risk compared to native populations. Managers assessing risk of specific trade pathways or trading partners should additionally consider the bridgehead status of the pest in addition to phytosanitary measures and more typical criterion. Risk assessments of species with limited invasion history should consider potentially drastic increases in propagule pressure with the establishment of bridgehead regions.

For modelling and forecasting efforts focused on newly emerging invasive pests, understanding the relationships between origin location, propagule pressure and invasibility is essential to making accurate predictions. The trade networks that guide global species flow display both small-world and scale-free properties (Banks et al. 2015), meaning that the removal of some nodes from the network can dramatically alter network topology. Thus, for All-Bridgehead species, because the trade network that facilitates their dispersal largely excludes pathways originating in the species' native range, the topology of the available trade network may be substantially different than if all pathways were equally utilised. When forecasting the spread of newly emerging species, modellers should consider implementing scenarios that include All-Bridgehead spread styles in addition to All-Native and Mixed-Range scenarios.

The correlation of bridgehead proportion with taxonomy suggests that related species often have similar responses to moving from native to non-native regions. Thus, if widely established species are known to display high population densities or propagule pressures in their non-native range, their close relatives may be more likely to display similar behaviour if they become invasive in the future. Phytosanitary organisations and other managers should particularly assess the risks of close relatives of known invaders.

Acknowledgements

The authors thank Rebecca Turner for providing interception data from MAAF in Japan and to Barney Caton for providing APHIS PIN data.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code supporting this paper along with other supplemental are available on Zenodo https://doi.org/10.5281/zenodo.12690178 and referenced as Worm et al. (2024) throughout the manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.