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Abstract

Aim: The Hemiptera is the fifth-largest insect order but among non-native insect species is approximately tied with the Coleoptera as the most species-rich insect order (Hemiptera comprise 20% more species than in world fauna). This over-representation may result from high propagule pressure or from high species invasiveness. Here, we assess the reasons for over-representation in this group by analysing geographical, temporal and taxonomic variation in numbers of historical invasions.

Location: Global.

Method: We assembled lists of historical Hemiptera invasions in 12 world regions, countries or islands (Australia, Chile, Europe, New Zealand, North America, South Africa, South Korea, Japan and the Galapagos, Hawaiian, Okinawa and Ogasawara Islands) and border interception data from nine countries (Australia, Canada, European Union, United Kingdom, Hawaii, Japan, New Zealand, South Korea, USA mainland and

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South Africa). Using these data, we identified hemipteran superfamilies that are historically over-represented among established non-native species, and superfamilies that are over-represented among arrivals (proxied by interceptions). We also compared temporal patterns of establishments among hemipteran suborders and among regions. **Results:** Across all regions, patterns of over- and under-representation were similar. The Aphidoidea, Coccoidea, Aleyrodoidea, Cimicoidea and Phylloxeroidea were over-represented among non-native species. These same superfamilies were not consistently over-represented among intercepted species indicating that propagule pressure does not completely explain the tendency of some Hemiptera to be over-represented among invasions. Asexual reproduction is common in most over-represented superfamilies and this trait may be key to explaining high invasion success in these superfamilies. **Conclusions:** We conclude that both propagule pressure and species invasiveness are drivers of high invasion success in the Sternorrhyncha suborder (aphids, scales, whiteflies) and this group plays a major role in the exceptional invasion success of Hemiptera in general. The high historical rates of invasion by Sternorrhyncha species provide justification for biosecurity measure focusing on exclusion of this group.

KEYWORDS

biological invasions, disharmony, insect, invasiveness, non-native species, propagule pressure

1 | INTRODUCTION

Given the extreme global diversity of insects (estimated to range from 1 to 10 million species (Chapman, 2009, Stork, 2018)), it is not surprising that the number of known non-native insect species outnumber those from all other animal groups (Seebens et al., 2017); recent estimates of the number of established non-native insect species range from 4992 to 9835 (Bonnamour et al., 2023; Seebens et al., 2018; Turner, Blake, & Liebhold, 2021). The only group with more established non-native species is the plant kingdom with about 14,000 known established non-native species worldwide (Pyšek et al., 2017).

The insect order Hemiptera (aphids, scales, planthoppers, leafhoppers, cicadas, shield bugs, plant bugs and other groups) is ubiquitous in most terrestrial and aquatic ecosystems. Over 100,000 Hemiptera species have been described worldwide (Bartlett et al., 2018; Zhang, 2013). Even though this places the Hemiptera fifth in the ranking of insect orders by global species richness, it is approximately tied with the Coleoptera for the most non-native species globally. Liebhold et al. (2016) found that across all world regions, the number of Hemiptera species that are established non-native species is 20% greater than expected based on their proportional representation among insects worldwide. This pattern of over-representation among non-native species is observed among non-native insect assemblages in virtually all regions that have been studied (Liebhold et al., 2016; López et al., 2023; Yamanaka et al., 2015).

Many non-native Hemiptera species cause major impacts on agriculture and on natural ecosystems. The largest Hemiptera suborder Auchenorrhyncha contains groups such as cicadas, leafhoppers, treehoppers, planthoppers and spittlebugs, many of which are agricultural pests due to their feeding damage and their ability to transmit plant pathogens. The second largest suborder, Heteroptera, is the 'true bugs'. While many Heteroptera are beneficial due to their habits of preying on other insects, a large number are serious pests. For example, the brown marmorated stink bug, *Halyomorpha halys*, is native to East Asia but in invaded regions in North America, Europe and South America, it is a pest of agriculture as well as a nuisance to homeowners (because it seeks shelter in homes, often in large numbers). The suborder Sternorrhyncha is the third largest Hemiptera suborder and many species cause immense damage to agriculture around the world. These include a multitude of aphid and scale insects that, due to their impacts on agriculture, pose risks to food security worldwide (Dedryver et al., 2010; Kondo & Watson, 2022). In forests and other natural ecosystems, many Sternorrhyncha (e.g. aphids, adelgids and scales) cause substantial damage (Branco et al., 2023; Causton et al., 2006). A particularly large fraction of hemipteran pests of agriculture and forestry are non-native species (Aukema et al., 2011; Miller et al., 2005). Although modern biosecurity measures have reduced invasion risks, it is likely that pest Hemiptera species will continue to be introduced accidentally to new regions in the future (MacLachlan et al., 2021). Given these risks, a better understanding of global patterns of historical Hemiptera invasions

is needed to inform improved biosecurity strategies for their exclusion.

Here, we hypothesize three processes which may explain the over-representation of Hemiptera among insect invasions worldwide: (1) propagule pressure, (2) invasiveness, (3) reporting bias (Table 1). Plant-feeding Hemiptera are generally small and commonly transported accidentally with imported live plants (Fenn-Moltu et al., 2023; Liebhold et al., 2012; Smith et al., 2007) and fruit, especially in passenger baggage (Liebhold et al., 2006). These pathways could facilitate high propagule pressure and subsequent frequent invasions. Another possibility is that Hemiptera are more adept at establishing than other insect orders (i.e. high invasiveness). A large number of hemipterans are capable of reproducing asexually (Simon et al., 2002; Vershinina & Kuznetsova, 2016), which can facilitate establishment in small founding populations by eliminating Allee effects associated with mate-finding (Rubio-Meléndez et al., 2019). Finally, because so many non-native Hemiptera are agricultural or forest pests, their occurrence may be more likely reported, thus resulting in their over-representation among reported invasions.

Numbers of native species can serve as a baseline for comparing numbers of non-native species among regions and among taxa. Native species richness may reflect the diversity of available niches (Nakadai, 2017; Ricklefs & Marquis, 2012), and therefore, it can be anticipated that non-native species richness would be correlated with native species richness. Conversely, the diversity-invasibility hypothesis posits that native species diversity confers resistance

to invasions (Levine & D'Antonio, 1999) and would, therefore, predict an inverse relationship between native and non-native richness. However, empirical support for the diversity-invasibility hypothesis is inconsistent (Fridley et al., 2007) and largely limited to plants (Pyšek et al., 2008). Few studies have investigated the effect of native insect species richness on insect invasions, but limited numbers of analyses support a positive relationship which is the opposite of that expected from the diversity-invasibility hypothesis (Borges et al., 2006; Marini et al., 2011).

Here, we assemble data on historical invasions by Hemiptera in 12 world regions to apply macroecological analyses that provide insight into why there are so many Hemiptera invasions. We use these data to compare the over-representation of various Hemiptera taxa within regional non-native assemblages and how these patterns can be explained by processes listed in Table 1. Specifically, we hypothesize that: (1) numbers of non-native species in each taxa are correlated with numbers of native species in the same taxa, (2) certain taxa are consistently over-represented within non-native assemblages compared to their representation within native assemblages across all regions, (3) taxa that are over-represented among non-native species are also over-represented in terms of propagule pressure (proxied by border interception frequencies), (4) rates of invasion by certain hemipteran taxa have changed over time. Resolving these questions would provide insight into understanding how propagule pressure and invasiveness contribute to determining why certain groups of organisms are more frequent invaders than others.

TABLE 1 Candidate processes that may contribute to the over-representation of certain Hemiptera taxa and the Hemiptera in genera.

General process	Specific mechanisms	Previous evidence	Evidence reported here
Propagule pressure	<ul style="list-style-type: none"> High incidence of arrival with imported plants Small body size difficult to detect during inspections 	<ul style="list-style-type: none"> Hemiptera dominate species intercepted with imported plants (Liebhold et al., 2006, 2012) 	<ul style="list-style-type: none"> Most superfamilies over-represented among established non-native species (Figure 3a) are also over-represented among species intercepted (Figure 3b).
Invasiveness	<ul style="list-style-type: none"> High incidence of asexual reproduction that facilitates establishment of small founding populations High reproductive rate and short generation time that facilitates rapid population growth 	<ul style="list-style-type: none"> Asexual reproduction is common in the Hemiptera compared to other insect orders (Simon et al., 2002; Vershinina & Kuznetsova, 2016) 	<ul style="list-style-type: none"> Most of the superfamilies over-represented among established non-native species (Figure 3a) exhibit a high frequency of asexual reproduction (Simon et al., 2002; Vershinina & Kuznetsova, 2016) Most of the superfamilies over-represented among established non-native species exhibit rapid population growth (e.g. Kindlemann et al., 2007)
Reporting bias	<ul style="list-style-type: none"> Many Hemiptera species are serious pests and may be reported earlier 	<ul style="list-style-type: none"> While many species have high impacts on agriculture and are unlikely to remain unnoticed, most species are not pests and are not likely to be discovered earlier than most other insect species Given small body sizes, many species go unnoticed for many years Several examples of long delays between establishment and discovery (MacLachlan et al., 2021) 	<ul style="list-style-type: none"> None

2 | METHODS

2.1 | Historical invasions in each region

We compiled lists of established non-native Hemiptera species, including year of first discovery, in 12 different regions worldwide (Figure S1) selected based on the existence of comprehensive lists described below. Lists may exist for several other countries from sources such as The Global Register of Introduced and Invasive Species (<https://griis.org>); however, in most cases, these lists are incomplete, and therefore, we chose not to use that information. The 12 regions for which we compiled lists were: Australia, Chile, Europe (including its major islands and the European part of Russia), the Galapagos Archipelago, the Hawaiian Archipelago, Japan (excluding outlying islands), New Zealand, North America (Canada, continental USA), the Ogasawara Islands (also known as Bonin Islands, Japan), Okinawa (Nansei Islands), South Africa and South Korea. The primary source for these lists was the International Non-native Insect Establishment Database (Turner, Blake, & Liebhold, 2021). See Turner, Blake, and Liebhold (2021), Liebhold et al. (2021) and Mally et al. (2022) for descriptions of the sources used to compile this database. This database was updated using records from a variety of sources, notably Dowell et al. (2016) for the North American list, the Galapagos Species Database (Charles Darwin Foundation, 2023) for the Galapagos Islands list and Matsunaga et al. (2019) for the Hawaii list. Data for South Africa were added from Picker and Griffiths (2017) and Zengeya and Wilson (2020). Data for Chile were added from López et al. (2023).

Lists of species established in each region were standardized based on the GBIF backbone taxonomy (GBIF Secretariat, 2021) to overcome duplication due to the existence of synonyms and misspellings. This taxonomic 'cleaning' was performed using the GBIF taxonomic database and the 'rGBIF' package in the R programming language (R Core Team, 2021). For the majority of hemipteran species, user-supplied names were recognized (including as synonyms or misspellings) by GBIF. A small fraction was not recognized so standardization was performed manually via searches of alternative databases and manual researching of names. A full list (including higher taxonomic information and year of discovery) of species established in each region is available from a Dryad data repository at <https://doi.org/10.5061/dryad.7m0cfxq2v>.

Prior to analyses, we removed records for species that were intentionally released (41 species; e.g., for the purpose of biological control), or species that were only established indoors (56 species; e.g., within a greenhouse). Records of established non-native species that were only recorded at the genus were also excluded. We recognize that lists of established non-native species may be incomplete, as there typically are lags between establishment, discovery and reporting of new non-native species (Morimoto et al., 2019).

For purposes of exploring factors affecting numbers of non-native Hemiptera species, in each superfamily in each region, we estimated a Poisson regression model of non-native species richness with superfamily, region and native species richness as explanatory

variables. To visualize which regions had proportionally more non-native Hemiptera species, we generated a scatterplot of total numbers of native Hemiptera species versus numbers of non-native Hemiptera species in each of the 12 studied regions. Numbers of native Hemiptera species in each superfamily in each of the 12 regions were compiled from sources listed in Table S1 and counts are given in Table S2. As a reference, we plotted the line under the expectation of a constant fraction of non-native species.

2.2 | Temporal patterns of invasions

The timing of Hemiptera species establishments was quantified using data described above for the eight regions with the greatest number of established non-native species: Australia, Chile, Europe, the Galapagos Archipelago, the Hawaiian Archipelago, Japan, New Zealand and North America. Data from South Africa, Okinawa, Ogasawara and South Korea lacked sufficient numbers of records with years of discovery to meaningfully characterize temporal trends. We acknowledge that year of initial establishment is typically unobserved so the year when a species is first discovered may occur after a lag of many years (Crooks, 2005; Essl et al., 2011); consequently, temporal patterns in discovery dates are likely to lag behind temporal patterns of establishment.

For each region, the total number of species established per decade (1890–2010) was calculated. The presence of a temporal trend in establishments was investigated by fitting a linear model of numbers of species as a function of decade for each region. The significance (critical value of $p = .00625$ based on a Bonferroni correction for multiple [8] comparisons) of the slope parameter from zero was interpreted as indicative of a temporal trend. We also plotted total numbers of species establishments (proxied by year of first discovery) per decade (1850–2020) for each suborder in each region.

2.3 | Proportional representation of superfamilies among invasions

Numbers of non-native species in each region were summarized at the superfamily level. These numbers were compared to numbers of native species in each superfamily from the same region. Numbers of native species per region were compiled as the sum of numbers of native species per family found in the sources listed in Table S1. For each region, scatterplots were made of numbers of native species versus numbers of non-native species for each superfamily. For reference, we plotted the expected number of species per superfamily assuming an equivalent proportion of non-native species relative to numbers of native species.

Similarly, we pooled numbers of non-native species established in each superfamily across all 12 regions and plotted these against the total numbers of described species in the superfamily worldwide. Again, we plotted the expected number of species per superfamily assuming an equivalent proportion of non-native

species relative to numbers of native species. We also plotted a region around this line indicating where the probability that a superfamily was over- or under-represented (when they fell outside the boundaries) was less than or equal to $\alpha=0.01$. We used a Bonferroni correction for the multiple comparisons, so the boundaries of this region were calculated as the upper and lower quantiles of the binomial distribution such that $(1 - \alpha/m) \times 100\%$ of the distribution lay within the boundary, where m is the number of superfamilies compared.

2.4 | Proportional representation of superfamilies among arrivals

We used border interception data as a proxy for propagule pressure for each superfamily (based on the 24 superfamilies with any interceptions). These data were derived from government biosecurity inspections made at ports in Australia, Canada, Europe, the Hawaiian Islands, Japan, New Zealand, South Africa and the USA mainland. Data consisted of records of non-native organisms intercepted during inspections of air and sea cargo, maritime vessels, international passenger baggage and international mail/courier parcels. A detailed description of these data is provided in Turner, Brockerhoff, et al. (2021) with differences/additions described in Table S3.

Numbers of species intercepted (across all countries) in each hemipteran superfamily were plotted against worldwide numbers of described species in each superfamily. For reference, we plotted the line showing an expected number of species per superfamily assuming an equivalent proportion of species intercepted relative to numbers of world species. We also plotted a region around this line indicating where the probability that a superfamily was over- or under-represented (when they fell outside the boundaries) following the same procedures described above.

3 | RESULTS

3.1 | Historical invasions in each region

A total of 1691 non-native Hemiptera species are known to have established successfully in at least one of the 12 study regions. The Auchenorrhyncha is the most species-rich hemipteran suborder worldwide (43,691 described species), followed by the Heteroptera (39,602 species), then the Sternorrhyncha (17,640) and the smallest suborder is the Coleorrhyncha (30 species). However, among the 12 world regions, the suborder with the most established non-native species was the Sternorrhyncha (1027 species) followed by the Heteroptera (375 species), and the Auchenorrhyncha (288 species). Only a single non-native Coleorrhyncha species has been identified as established (the Australian mossbug *Hemiodoecus leai* which is only known to have invaded New Zealand (Wakelin & Lariviere, 2014)).

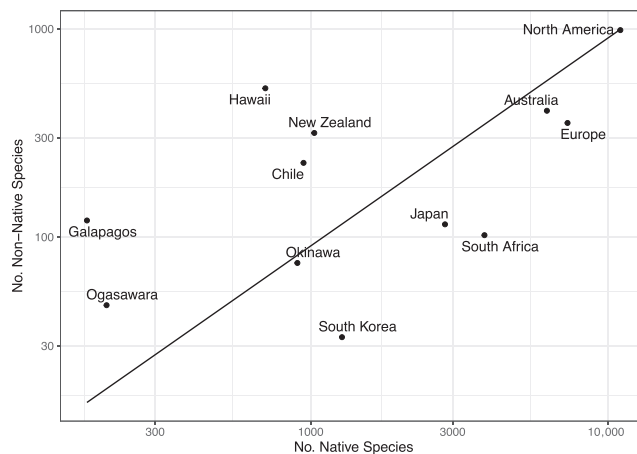


FIGURE 1 Total number of native versus non-native Hemiptera species in each of the study regions. Black line represents the expected number of non-native species if the relative number of non-native Hemiptera species in a region is the same as the relative number of natives in the same region.

Based on the Poisson regression model, we found that non-native species richness was affected by native species richness ($\chi^2 = 14.6$, $p = .000131$), superfamily ($\chi^2 = 4620.0$, $p < 2.2e-16$) and region ($\chi^2 = 1709.0$, $p < 2.2e-16$). The effect of native species richness on non-native richness was positive (estimated coefficient 0.000187). North America has the greatest number of both native (10,981) and non-native hemipteran species (985) (Figure 1). The percentage of Hemiptera present in a region that are non-native is highest in the Galapagos Islands (43%) and the Hawaiian Islands (42%). The proportion of hemipteran species that are non-native is lowest in Europe (4.6%), Japan (3.9%) and South Korea (2.5%).

3.2 | Temporal patterns of invasions

Temporal patterns of numbers of species discoveries in each region per decade are shown in Figure 2. Relatively few non-native Hemiptera species were reported in any of the eight regions prior to 1850 (1 in Australia, 1 in Chile, 13 in Europe, 1 in the Galapagos, 0 in Hawaii, 1 in Japan, 0 in New Zealand and 11 in North America). In all regions except Chile, discovery records dropped in 2020 (likely due to delays in reporting). The peak number of species discovered per decade occurred in the 1900s in Australia and Hawaii, 1920s in North America, 1960s in New Zealand, 1990s in Chile, 2000s in Europe and Galapagos and 2010s in Japan. There was a significant upward trend of species discoveries in both Chile and Europe; an increasing slope was marginally greater than zero in the Galapagos Islands (Table S4). Numbers of Sternorrhyncha species generally exceeded those of Auchenorrhyncha and Heteroptera in all years in every region (Figure 2). Historical Sternorrhyncha discoveries were visually suggestive of a bimodal temporal distribution in Hawaii, Japan and New Zealand.

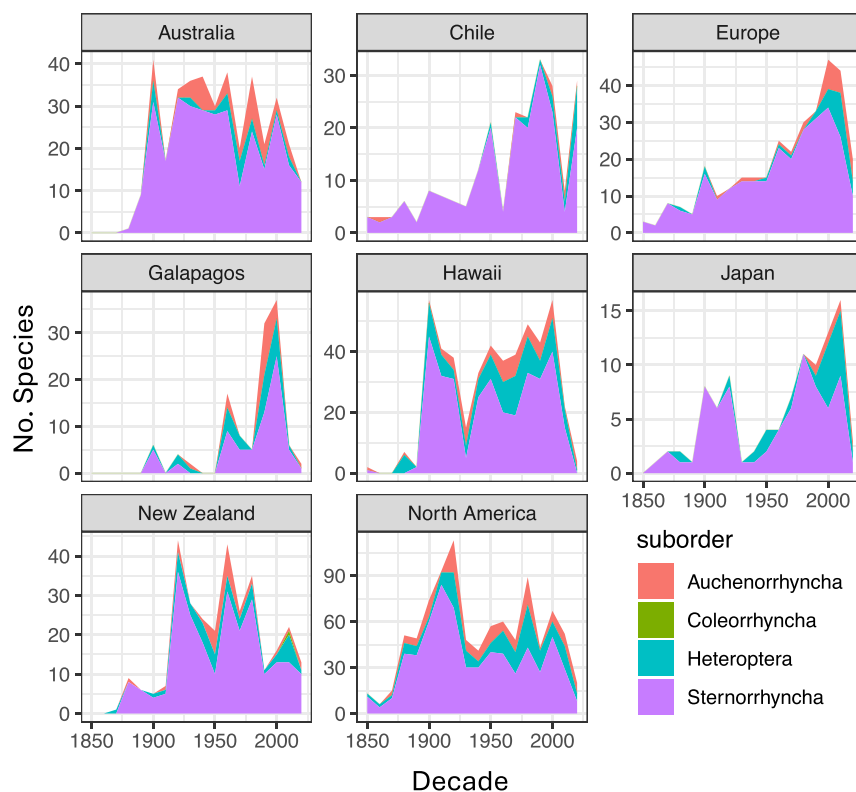


FIGURE 2 Numbers of non-native species discovered (proxy for establishment) each decade from 1850 to 2020.

3.3 | Proportional representation of superfamilies among invasions

Although the Membracoidea is the most species-rich superfamily worldwide, there are more non-native Aphidoidea (430) and Coccoidea (427) established across the 12 world regions (Figure 3a). The Aphidoidea, Coccoidea, Aleyrodoidea, Cimicoidea and Phylloxeroidea were all significantly over-represented among the pooled (among the 12 regions) non-native assemblage compared to their representation among the world's Hemiptera fauna. Of these, all but the Cimicoidea are in the suborder Sternorrhyncha. The Membracoidea, Miroidea, Fulgoroidea, Pentatomoidea, Reduvoidea, Cercopoidea, Aradoidea, Gerroidea and Cicadoidea were all under-represented; five of these superfamilies are Heteroptera and the remaining four are Auchenorrhyncha (all Auchenorrhyncha included in the analysis were under-represented).

The 12 regions showed generally similar patterns of over- and under-representation of the number of non-native species compared to regional numbers of native species in each superfamily (Figure 4). The Aphidoidea, Coccoidea and Aleyrodoidea tend to be over-represented among non-native species in each region. Perhaps the most extreme case of over-representation is seen with the Aphidoidea in Australia, where there are 153 established non-native Aphidoidea as opposed to only 23 native species. There are zero native Aphidoidea and Aleyrodoidea described from Hawaii but 114 and 35 non-native species in these two superfamilies established there respectively. The Lygaeoidea and Fulgoroidea tend to be under-represented among non-natives in all regions, with the

noticeable exception of South Korea where Fulgoroidea was the most species-rich superfamily among non-natives.

3.4 | Proportional representation of superfamilies among interceptions

Numbers of species intercepted, along with numbers of described world species in each hemipteran superfamily are shown in Table S5. The Coccoidea, Pentatomoidea, Lygaeoidea, Aphidoidea, Aleyrodoidea, Coreoidea, Tingoidea and Pyrrhocoroidea were all over-represented among border interceptions compared to their proportions in the world Hemiptera fauna (Figure 3b). There was a tendency for Auchenorrhyncha to be under-represented among interceptions. While the Aphidoidea, Coccoidea and Aleyrodoidea are over-represented among established non-natives (Figure 3a) and among intercepted species (Figure 3b), the Pentatomoidea is over-represented in interceptions but under-represented in establishments. The Lygaeoidea, Coreoidea and Tingoidea are over-represented among interceptions but neither over- nor under-represented among establishments.

4 | DISCUSSION

About 100,000 hemipteran species are described worldwide, placing this order fifth in global species richness among insect orders after Coleoptera, Lepidoptera, Diptera and Hymenoptera

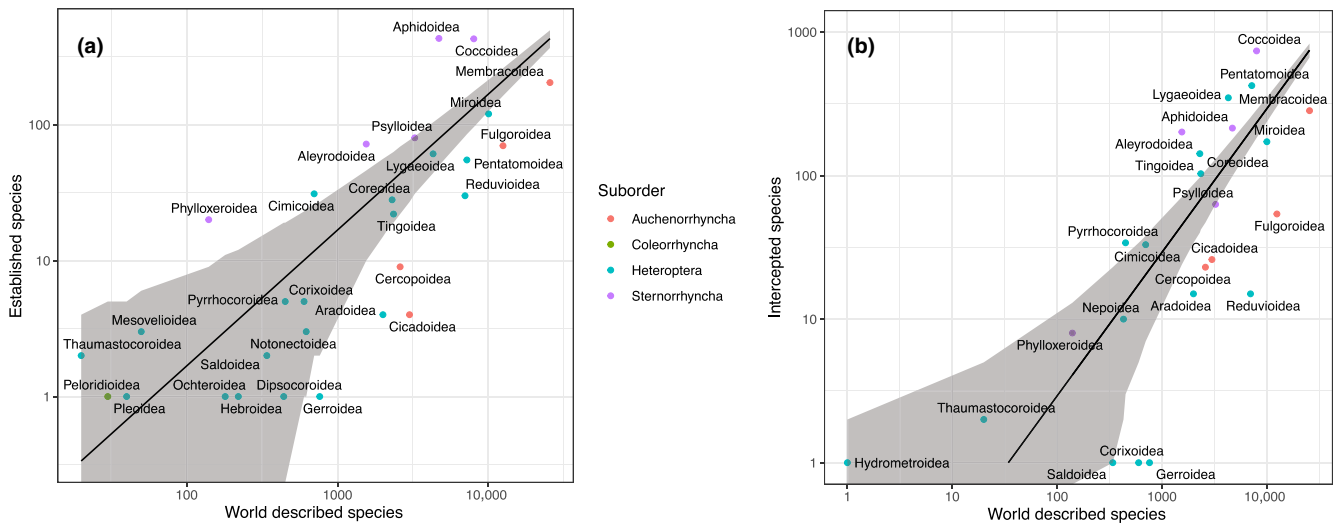


FIGURE 3 Over- and under-representation of non-native Hemiptera superfamilies. (a) Total number of established non-native Hemiptera species in all 12 regions versus world species richness for each superfamily. (b) Total number of Hemiptera species intercepted (during border inspections) in Australia, Canada, Europe, the Hawaiian Islands, Japan, New Zealand, South Africa and the USA mainland versus world species richness for each superfamily. The black line describes the expected numbers of non-native species per superfamily under the assumption that their proportional representation among non-native Hemiptera is the same as the proportional representation of that superfamily among all world species; grey shading indicates the $\alpha=0.01$ level (under a binomial distribution and with a Bonferroni correction to account for the number of superfamilies compared), with labelled families outside this area considered over- or under-represented.

(Stork, 2018; Zhang, 2013). Despite this ranking, a variety of studies of non-native species composition in most world regions consistently rank the Hemiptera as the most species-rich order among non-native species (Liebhold et al., 2016; López et al., 2023; Nahrung & Carnegie, 2020; Picker & Griffiths, 2017; Sailer, 1978; Yamanaka et al., 2015). The Hemiptera also comprises the most frequently intercepted insect order at ports (McCullough et al., 2006; Turner, Brockerhoff, et al., 2021). This is due, in part, to their ubiquitous presence on imported live plants (Liebhold et al., 2012) as well as on fruits and vegetables, especially such plant material carried in air passenger baggage and mail (Fenn-Moltu et al., 2023; Liebhold et al., 2006). However, it is not clear if this high rate of transport with trade alone explains their status as the most widely established order among non-native insect species. Our results indicate that high propagule pressure combined with invasiveness traits for several highly species-rich superfamilies of Hemiptera are the cause for the observed over-representation of the Hemiptera among non-native species.

Patterns of over- and under-representations of non-native species across Hemiptera superfamilies were similar in all 12 investigated world regions (Figure 4), consistent with patterns observed when data from all regions are pooled (Figure 3a). The Sternorrhyncha, particularly the Aphidoidea, Coccoidea and Aleyrodoidea, are all over-represented among non-native assemblages. Their over-representation among intercepted species (Figure 3b) also suggests that the ubiquity of these groups among non-native species may at least partly relate to their high propagule pressure. Indeed, Turner et al. (2020) showed that establishment status of individual non-native species in the Aphididae can be predicted from their historical interception frequencies during port inspections. Sternorrhyncha

are known to be abundant in pathways associated with the international movement of fruit, vegetables and live plants transported either in cargo or passenger baggage (Fenn-Moltu et al., 2023; Kiritani & Yamamura, 2003; Liebhold et al., 2012). However, other superfamilies, such as the Pentatomoidea, Coreoidea and Lygaeoidea are over-represented among interceptions but not among establishments. Thus, consistently high propagule pressure (proxied by interceptions) does not necessarily translate into high probabilities of establishment among all Hemiptera. We note that border inspections often target certain groups so some caution should be exercised in comparing interception rates among taxa. One invasion pathway that is not proxied by interception data is windborne dispersal; many Hemiptera, especially the Sternorrhyncha, are small and frequently transported long distances (Holzapfel & Harrell, 1968; Loxdale et al., 1993). It is possible that prior to the last two centuries of globalization, transoceanic dispersing insects failed to establish alien populations as a consequence of the absence of hosts, but with recent trends of widespread establishment of cultivated and invasive plants, an increasing fraction of immigrating species are successfully established.

In addition to propagule pressure, variation in species invasiveness might explain observed patterns of over- and under-representation among hemipteran taxa. The field of invasion science is replete with inconsistent use of terminology, but here we use the term invasiveness to refer to inherent biological traits of a species that determine its ability to establish following arrival in a novel region (Van Kleunen et al., 2010) and note that this definition is inherently different from alternative definitions that refer to the capability of a species to cause damage (e.g., Zhao et al., 2023). Compared to the literature on plants, relatively few studies have explored traits

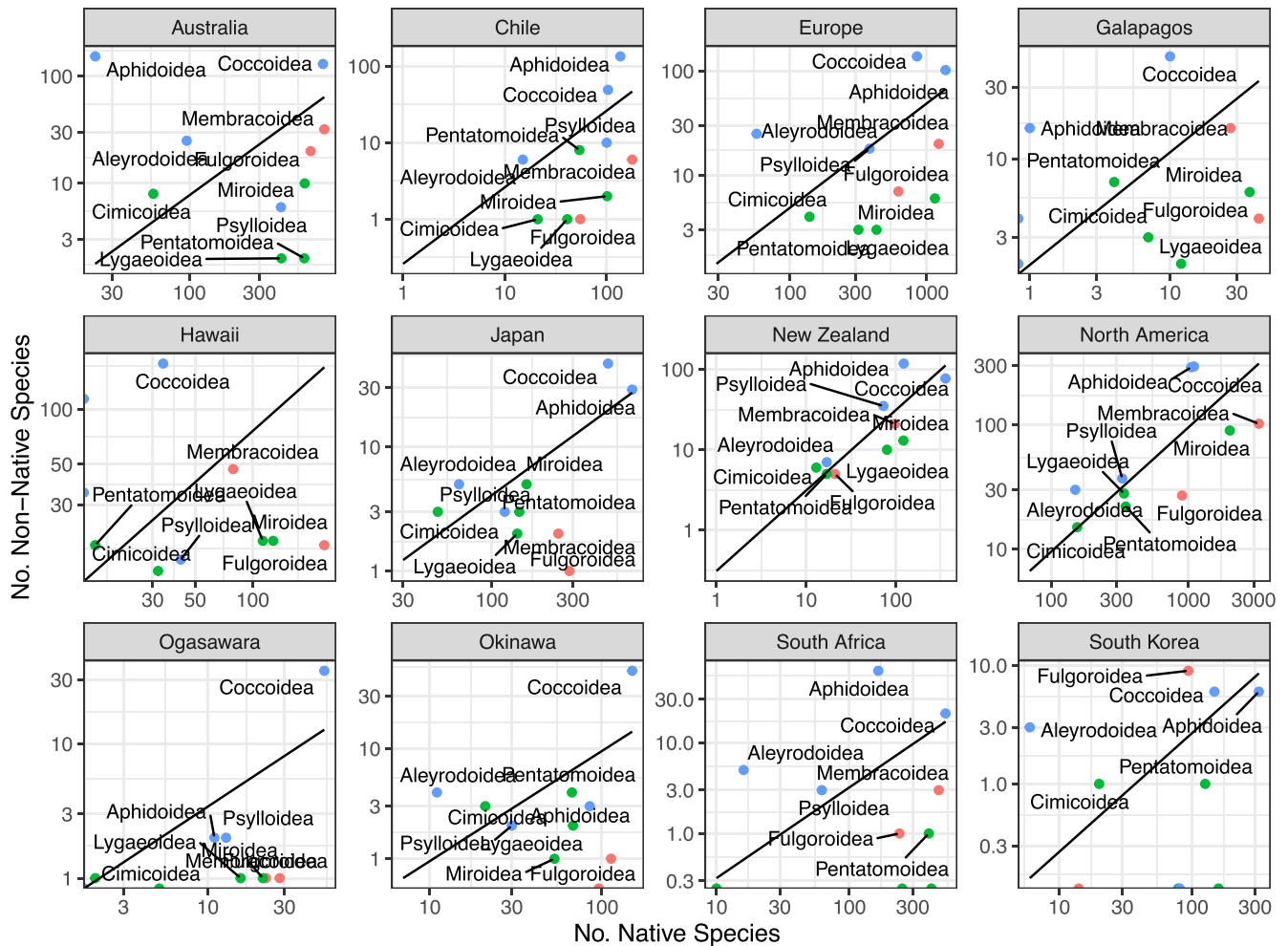


FIGURE 4 Number of non-native Hemiptera species versus native species richness for each superfamily in each of 12 regions. See [Figure 3](#) for suborder colour legend. The black line describes the expected numbers of non-native species per superfamily under the assumption that their proportional representation among non-native Hemiptera in that region is the same as the proportional representation of that superfamily among native Hemiptera in that region.

related to the invasiveness of insects (Pyšek et al., 2008), although the climatic tolerance of a species and its ability to utilize available hosts are critical ingredients to the ability of a species to establish (Segoli et al., 2023). Additional traits affecting the ability of arriving species to establish are those related to successful reproduction at low densities. Most accidentally introduced insect populations arrive as small numbers of individuals; Allee effects and stochastic dynamics play a large role in the successful establishment of such populations (Liebhold & Tobin, 2008). Mate-finding failure is a common cause of Allee dynamics in insects and consequently asexually reproducing insects typically exhibit weaker demographic Allee effects and are more likely to establish at low densities (Gascoigne et al., 2009). We note here that of the five hemipteran superfamilies identified as over-represented among non-native Hemiptera ([Figure 3a](#)), all but one (the Cimicoidea) are known to have a high incidence of asexual reproduction; Verzhinina and Kuznetsova (2016) identified high incidence of asexual reproduction in the Aphidoidea, Coccoidea, Psylloidea, Aleyrodoidea and Phylloxeroidea. In contrast, superfamilies in the suborder Auchenorrhyncha generally reproduce

sexually and are under-represented among non-native species. Thus, while high propagule pressure may be a necessary ingredient for invasion success in given taxa, the ability to reproduce asexually may explain why some species with high propagule pressure establish and others do not. Indeed, Ross et al. (2013) noted that across scale insects, asexual reproduction is particularly common in species that also exhibit high population sizes. High population size potentially translates into high propagule pressure so when combined with asexual reproduction, this creates a 'perfect storm' of invasion success in these groups. Though not all Hemiptera are capable of asexual reproduction, the overall results indicate that the coincidence of high propagule pressure and asexual reproduction may be the primary explanation for the high invasion success of the Hemiptera worldwide. We note that over-representation of the Cimicoidea may be related to their ectoparasitic association with mammals which may both promote propagule pressure (movement with humans and livestock) and invasiveness (they may easily find hosts upon arrival).

Among the factors explaining the exceptional success of Hemiptera species ([Table 1](#)), propagule pressure and invasiveness,

thus, remain the best candidates. Given their often small body sizes and long time lags between establishment and discovery, reporting bias remains an unlikely explanation for observed high invasion success in the Hemiptera (though we provide no direct analysis of reporting bias here).

The Sternorrhyncha are clearly over-represented among non-native insects (Figure 3a), but that pattern is less evident among Hemiptera species intercepted at ports (Figure 3b). The success of the Sternorrhyncha as invaders could be due to the prevalence of asexual reproduction noted above. But it also could reflect their small body size and their intimate physical association with their host plants, traits that may facilitate their successful association with imported host plants upon arrival in novel regions. Small body size in the Sternorrhyncha may also facilitate their movement via windborne dispersal. Data from different world regions indicate that establishments of Heteroptera and Auchenorrhyncha are beginning to 'catch-up' with the Sternorrhyncha (Figure 2). The reasons for this trend are not clear but it could be related to the development of new invasion pathways with changing global patterns of trade and travel which open new species pools to invasions or the depletion of source pools of Sternorrhyncha species (MacLachlan et al., 2021; Seebens et al., 2018).

The under-representation of the Cicadoidea in all regions (Figures 3a and 4) may be influenced by several factors. These species have long life cycles and are often host specific, so a lack of suitable host plants may lead to establishment failure following initial transport. The Cicadoidea also tend to be large and as a consequence are heavily preyed upon. Such predation may lead to the extinction of small founding populations. This was illustrated by Marlatt (1907) who attempted to introduce a population of periodical cicadas experimentally into a portion of North America where local populations were synchronized to emerge in a year different from the source population. Even though he introduced hundreds of thousands of nymphs which successfully fed on tree roots in experimental plots, no adults survived due to heavy avian predation decimating the population. Marlatt's (1907) experiment illustrated that even under optimal conditions, successful establishment of Cicadoidea is not guaranteed.

Given that the Hemiptera comprises the largest group of non-native insects throughout the world, it is not surprising that spatial and temporal patterns of Hemiptera invasions are representative of patterns seen for all non-native insects. The geographic variation in numbers of non-native Hemiptera species reported here (Figure 1) largely mirrors the geographic variation in total numbers of non-native species worldwide. For example, North America and Hawaii have the greatest numbers of non-native Hemiptera species and also have more non-native insects in total (pooled across all orders) than any of the other regions (Liebhold et al., 2018).

The positive effect of native Hemiptera richness on non-native richness indicates that the biotic resistance hypothesis (also known as the diversity-invasibility hypothesis) (Levine & D'Antonio, 1999) does not apply in this system. It also is in agreement with the few other studies that have investigated this relationship in insects

(Borges et al., 2006; Marini et al., 2011). Higher native insect species richness likely reflects a greater diversity of available niches that facilitate establishment of arriving non-native insect species. Compared to plants (which provide the best examples of the diversity-invasibility hypothesis) direct interspecific competition is generally less important for insects (Kaplan & Denno, 2007) and this means that establishment of non-native insects is unlikely to be adversely affected by competitive effects of native species. We also note that most of the regions where non-native species comprise the largest fraction of Hemiptera species are islands (Figure 1); Moser et al. (2018) found consistently more non-native species with increasing insular isolation across a variety of plant and animal taxa though Liebhold et al. (2018) did not find any effect of insularity on total non-native insect richness.

Temporal patterns of Hemiptera discoveries in each region (Figure 2) also mirror temporal patterns of establishments described in other studies for insects in general. For example, the significant trend of increasing rates of non-native Hemiptera discoveries during the last five decades in Europe (Table S3) reflects the similar patterns described for all non-native insects established in that same region (Roques, 2010). Bimodal patterns of Hemiptera discoveries seen in Hawaii, New Zealand, North America and Japan (Figure 2) are similar to patterns previously seen in the discoveries of all insects and may reflect temporal variation in propagule pressure driven by the two historical waves of globalization during the previous two centuries (Bonnamour et al., 2021). It should be noted again that there is typically a lag between a species' establishment and its discovery and that temporal variation in discovery effort (e.g. such as caused by variation in numbers of taxonomists studying a particular group) may obscure the use of time series of discoveries as a proxy for temporal patterns of establishments (McGeoch et al., 2023). There has been progress in the development of statistical methods for inferring temporal patterns of establishment from discovery data (Buba et al., 2024; MacLachlan et al., 2021) but even without applying such methods, the marked differences in temporal patterns of discoveries over the last 170 years seen here (Figure 2) most likely reflect differences in temporal patterns of establishment.

Previous studies have noted historical decreases in rates of establishment of certain Hemiptera groups such as scales and insects in North America (Liebhold & Griffin, 2016; Miller et al., 2005; Skvarla et al., 2017). Though we did not detect significant downward trends in species discovery rates, we notably did not observe any increases in discovery rates in regions such as Australia, New Zealand and Hawaii (Figure 2) despite increased imports to these regions. This may reflect biosecurity measures in these countries that have had positive impacts on minimizing new species establishments. MacLachlan et al. (2021) applied a model accounting for discovery lags and temporal variation in discovery effort to data on plant-feeding Hemiptera discovered in North America and found that establishment of species originating from the Asian and European Palearctic regions (where most of these species originated) have conspicuously declined despite increases in imports from these regions. Such patterns could also result, in part, from the depletion

of pools of highly invasive species from source regions as a result of successive invasions (Liebholt et al., 2017; Seebens et al., 2021). However, Nahrung et al. (2023) pointed out that while successful exclusion of individual invading species as a result of biosecurity measures is often invisible, the failure of insect establishments to track increases in imports in selected regions may represent visible success of these measures.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.




PEER REVIEW


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DATA AVAILABILITY STATEMENT

A full list (including taxonomic information and year of discovery) of species established in each region is available from a Dryad data repository at the following link: <https://doi.org/10.5061/dryad.7m0cfxq2v>.

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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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