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Research Article

Insect invasion success depends on taxon and trophic group

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Abstract

The majority of non-native animal species globally are insects, though some insect species are more successful invaders than others. These differences can be attributed, in part, to differences among dominant trophic groups. Previous analyses indicate that insect herbivores are generally over-represented among non-native species while other groups, such as predators, are under-represented. Here we explore how invasion success varies among insect taxa and trophic groups. We quantify over-representation in species grouped by taxon (order or family) and larval trophic group (herbivore, detritivore, predator, parasite, brood carer); over- and under-representation is computed by comparing proportional representation of groups among non-native species in 12 world regions with total numbers in these same groups globally. Although herbivores are generally the most successful group among non-natives, we found their invasion success to vary among their taxonomic groups: herbivores are over-represented among Hemiptera, Diptera, Thysanoptera and Hymenoptera, but under-represented among Lepidoptera and Orthoptera; similar patterns are seen at the family-level within orders. Even after accounting for trophic group, some orders were still over-represented. Within trophic groups, this pattern appeared strongest for herbivores, where predominantly parthenogenetic families belonging to the Hemiptera and Thysanoptera were over-represented in non-native assemblages, while families in the Lepidoptera and Polyneoptera were under-represented. Over time (1850s to 2000s), fractions of non-native species numbers in certain orders and trophic groups have varied, such as among parasites, where a considerable turnover took place from mostly bird-lice (Psocodea) in the 19th century to parasitic wasps (Hymenoptera) in the 20th century. It is thus likely that factors other than trophic group, such as associations with invasion pathways (e.g., plants, wood packaging), cause the observed differences in the over-representation of families belonging to different orders.

Key words: Brood carer, detritivore, feeding guild, herbivore, invasion disharmony, non-native species, parasite, predator

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Introduction

Insects are the second-largest group of non-native organisms worldwide (after plants) (Seebens et al. 2017). Insects are also the most diverse group of animals globally, with more than one million described species and an estimated 4.5 million undescribed species (Stork 2017). Their success as a group is attributed to several factors, such as features of their body and development (miniaturisation, wings, mouthpart diversity, full metamorphosis), ecological niche specialisation, capacity for rapid speciation, low rates of natural extinction, and their geological age, dating back to the Early Devonian around 419–393 million years ago (Grimaldi and Engel 2005; Mayhew 2007; Dunlop and Garwood 2017). The dominant life history of preimaginal stages is herbivory, with an estimated one third to one half of all species feeding on various parts of plants (Jermy and Szentesi 2021; Mally et al. 2024). The predominance of this feeding mode is most likely a result of their co-evolution alongside the diversification of angiosperm plants (Ehrlich and Raven 1964), which has contributed to the radiation of plant-feeding groups such as moths and butterflies (Labandeira et al. 1994; Wahlberg et al. 2013), phytophagous beetles (Phytophaga) (Farrell 1998), most Hemiptera (Vea and Grimaldi 2016; Ye et al. 2022), and ancestral wasp lineages (Symphyta) (Isaka and Sato 2014; Nyman et al. 2019).

Herbivores are disproportionately more prevalent among non-native insects than among all insects worldwide (Mally et al. 2024), indicating "invasion disharmony", i.e., systematic compositional differences between native and non-native assemblages as a result of species filtering during biological invasions (Liebhold et al. 2021). This pattern, along with the temporal lag (Bonnamour et al. 2023) and geographical association (Liebhold et al. 2018) of historical insect invasions with plant invasions, supports the hypothesis that plants play a driving role in the establishment success of non-native insects. A large fraction of herbivores are host-specific (Forister et al. 2015), and introductions of non-native plants create niches for non-native insects, thereby facilitating their invasions (Bertelsmeier et al. 2024).

In contrast, most detritivores are generalists, capable of feeding on a diverse array of dead plant and animal material. Historically, stone and soil used as ballast in early maritime vessels served as pathways that facilitated the intercontinental introduction of soil-dwelling detritivores and predators (Lindroth 1957; Cárdenas and Buddle 2007). It therefore comes as no surprise that the earliest insect invasions were by detritivores and predators (Panagiotakopulu and Buckland 2017), and even until relatively recently (e.g., 1600–1800), these trophic groups dominated among non-native insects (Mally et al. 2024). However, they were eventually outnumbered by a surge in herbivore invasions that was probably facilitated by introductions of non-native plants (Bonnamour et al. 2023), and in total, predators and detritivores are now under-represented among non-native insect assemblages worldwide (Mally et al. 2024).

Previous macroecological analyses have documented patterns in which specific insect groups are historically over-represented among non-native assemblages. Certain insect orders, such as the Hemiptera and Thysanoptera, are over-represented among non-native species compared to their relative representation among the global fauna, indicating high invasion success (Yamanaka et al. 2015; Liebhold et al. 2016). Moreover, within orders, certain families are over-represented among non-native insect species (Liebhold et al. 2021, 2024; Mally et al. 2022). Comparing trophic groups among insects, Mally et al. (2024) found that herbivores are

over-represented among non-native species worldwide. These patterns may result from invasion pathways filtering out specific groups of insects but also from the availability of ecological niches, such as those created by non-native plants that facilitate the establishment of arriving insect species (Bertelsmeier et al. 2024). However, within most insect orders and families, little is known about how and why certain groups of insects are more prone to invading than others. Information about which groups of insects are more likely to be transported and establish would be valuable in risk assessments to guide the implementation of biosecurity measures such as import prohibitions or mandatory phytosanitary treatments.

Here, we investigate historical patterns of invasion success among non-native insect species assemblages from 12 world regions to search for indications of invasion disharmony among five major larval trophic groups (herbivory, predation, parasitism, detritivory, and brood caring) within various insect orders and families. We further investigate changes in the proportions of different trophic groups within insect orders over 16 decades (1850s to 2000s) to reveal invasion patterns over time. We pose three hypotheses: 1) insect taxa with predominantly herbivorous larvae are over-represented among non-natives within individual insect orders; 2) within each trophic group, non-native species in all orders and families are equally represented relative to their global composition; 3) fractions of non-native species numbers within different orders and trophic groups have not varied over time.

Methods

Data

We used the International Non-native Insect Establishment Database (Turner et al. 2024) to source relatively comprehensive lists of non-native species for the following 12 world regions, spanning all continents except Antarctica (Fig. A1): North America (Canada, continental USA), the Hawaiian Islands, the Galápagos Islands, continental Chile, Europe (including its major islands and the European part of Russia), South Africa, South Korea, Japan, the Nansei Islands, the Ogasawara Islands, Australia, and New Zealand. While lists of non-native species are available from other regions, these generally are not comprehensive, and we avoided using them to prevent taxonomic and temporal bias. Species reported as eradicated or intentionally introduced were excluded from the analysis. Taxonomic cleaning was carried out based on the GBIF taxonomic backbone (GBIF 2021) using the R package rgbif v3.7.5 (Chamberlain et al. 2023); exceptions from the GBIF backbone taxonomy are listed in Suppl. material 1. Hereafter, we refer to this dataset of non-native species in the 12 world regions as the "non-native dataset".

For each record of a non-native species in a given region, the year of first discovery was included in our analyses, serving as a proxy for the year of establishment, which is unknown in most cases and predates the year of discovery (McGeoch et al. 2023). Records reported after 2009 were excluded, since these showed signs of reporting lag (Smith et al. 2018).

Numbers of global insect species were used as a baseline for quantifying the over- or under-representation of specific insect trophic groups among non-native species. Global numbers of described insect species per family and per order were compiled from various sources, indicated in Suppl. material 1. We restricted our analyses to families with at least 500 described species globally (called

"500+ families" hereafter) to limit the stochastic effects of species-poor families. Furthermore, insect families with predominantly aquatic larvae were excluded, as aquatic insects are systematically under-represented among non-native assemblages worldwide (Sendek et al. 2022). Hereafter, we refer to this family-level dataset of global numbers of insects as the "global dataset".

Based upon the mode of feeding of immature stages (i.e., larvae), we assigned a larval trophic group (LTG) to (a) each insect species in the non-native dataset and (b) each of the 500+ families in the global dataset. We standardised the classification on larval mode of feeding rather than adult feeding because (i) immature stages always feed, while in some taxa, no feeding occurs in the adult stage, and (ii) feeding during immature stages tends to be more extensive than during the adult stage for most insect species. This classification distinguishes five larval trophic groups (LTGs): herbivory, predation, parasitism, detritivory, and parental provisioning (i.e., brood caring).

"Herbivory" was assigned to all insect families with larvae feeding on living tissues of any type of land plants (embryophytes), excluding algae; this includes free-feeding folivores, leafminers, species boring in plant tissue (including seeds), sap-feeders and gall-makers. "Predation" was defined as larval feeding on freshly killed animal tissue of more than one prey item. This does not apply to the slow consumption of a single living animal host as seen in parasites. "Parasitism" comprises parasites, parasitoids (including hyperparasitoids) and kleptoparasites, and was defined as larvae feeding on or inside a single living animal host organism. This includes parasitoids with invertebrate hosts as well as parasites of vertebrates. Kleptoparasitic species do not readily fit into this definition, as the larvae feed on the provisions of plant or animal origin of their host (including preying on the host eggs and/or larvae). However, kleptoparasites often require a specific systematic group of hosts that they have adapted to and thus, from an invasion biology point of view, closely resemble the parasitism feeding guild. "Detritivory" encompasses larval feeding on detritus, dead and decaying animal and plant substrate, fungi, lichens and algae. Fungivory was included in the category of detritivory, as it is often difficult to ascertain whether an organism solely feeds on detritus or also (maybe exclusively) on fungal hyphae growing on the decomposing matter. "Parental provisioning" (brood caring) was applied to species that provide their larvae with food (animal- and/or plant-based), so that larvae do not actively forage for food in their environment but are dependent on parental provisions accumulated before and/or during larval development. We acknowledge that parental provisioning is a behaviour and not a trophic group; brood carers require a dedicated nest structure in their immature phases, either with sufficient food provided beforehand or with continuous feeding of the growing larva by the parent generation. From an invasion biology point of view, this adds complexity to the invasion pathway and distinguishes this group from the other four trophic groups. As stated above, kleptoparasites, although also engaging in brood care, were classified in the parasitism guild. Ambrosia beetles, although engaging in gardening of fungi on which the larvae feed, were not categorised as brood carers, but as fungivores (and thus included in detritivory).

While the trophic guild classification system that we applied here has been widely used in the past, we acknowledge the existence of other, more detailed classification systems that each have their own merit. However, we opted for this system, in part because of its simplicity but also because little or no information is available about the biology of many insect species, which prevents the implementation of more complex classification systems.

In the global dataset, we estimated the proportion of global species in each of the 500+ families that fell into each of the five trophic guilds, ranging from 0 (no known species in the LTG) to 1 (all known species in the LTG). For families with species falling into more than one LTG, we estimated the proportion of species in each LTG using increments of 0.1, or smaller increments when specific species numbers were available. Species numbers per LTG for each family ("family-LTG") were calculated by multiplying the relative proportion of each LTG by the family's global species number. For example, for Dermestidae, proportions of 0.8 for detritivores and 0.2 for predators were each multiplied by 1200 (the number of global Dermestidae species), resulting in family-LTGs of 960 global detritivorous species and 240 global predator species. Species per insect order were summed from the species in the families within a respective order. Insect families and orders with fewer than 500 species in a given LTG were excluded from further analyses.

In the non-native dataset, species were automatically assigned the LTG of their family if all species in that family were known to occupy a single LTG. For example, the aphid *Aloephagus myersi* is classified as an herbivore since all Aphididae species are herbivores. However, for species in "mixed" families (e.g. Staphylinidae contains herbivores, predators, detritivores and parasites) it was necessary to categorise each non-native species by searching the literature. Species occupying more than one LTG because of their mixed diet were split into equal fractions of 1 (e.g., *Sinoxylon unidentatum*, a bostrichid beetle, was classified as 0.5 detritivore and 0.5 herbivore).

Proportions of trophic guilds compared between native and non-native assemblages

We compared observed and expected numbers of non-native species based on numbers of global species per LTG for different insect orders. The expected number of species per LTG was calculated assuming an equivalent proportion of species in each LTG in the global species assemblage. To illustrate variation in invasion disharmony among insect orders, we generated scatterplots of numbers of non-native species per family-LTG against numbers of species in the same family-LTG for the global assemblage. The scatterplots include a line of equivalent proportions as well as significance bounds about this line, which were calculated as the 99% quantiles of the binomial distribution. Any family-LTGs which fell outside these bounds were deemed over- or under-represented at the $\alpha = 0.01$ level, using a Bonferroni correction (Dunn 1961) to account for multiple comparisons among families. A similar scatterplot was generated comparing non-native with global species richness in the order-level LTGs summed from the families in a respective order.

To investigate differences among insect orders within the five LTGs, we fitted a negative binomial regression model to variation in numbers of non-native species in each family as a function of numbers of global species in the same family using the glm.nb function in the MASS package (Venables and Ripley 2002) of R (R Core Team 2021). Separate models were estimated for each LTG. We then calculated the pairwise comparisons of the estimated marginal means among orders using the emmeans() function in the emmeans package (Lenth 2024) and illustrated the results, including significant differences between orders within an LTG. To minimise the effects of species-poor orders, we pooled Blattodea, Mantodea, Orthoptera and Phasmatodea into Polyneoptera.

Numbers and proportions over time

Temporal trends of insect orders in the five LTGs were quantified both as invasion rates (numbers of new species recorded as established per decade) and as cumulative numbers of species over time in each order, pooled from the twelve world regions. Blattodea, Mantodea, Orthoptera and Phasmatodea were pooled into Polyneoptera. Occurrences of non-native species in more than one of the twelve world regions were considered independent invasion events. Again, records reported after 2009 were excluded (see above). To test for changes in LTG proportions over time, we used the cumulative sums from the last year of each decade (1859, 1869 etc. for the five LTGs) and employed Cochran-Armitage tests for trend over time using the R package DescTools (Signorell 2024). Invasion rates of the six insect orders with the most non-native species among the 12 pooled world regions were calculated as moving averages (averaged across two-decade windows) of newly recorded non-native species per decade (1850s to 2000s). Trends over time among invasion rates per LTG per order were investigated with Mann-Kendall tests using the R package Kendall (McLeod 2022). Invasion rates were illustrated as line plots. All illustrations were generated using the tidyverse package collection (Wickham et al. 2019) in RStudio (RStudio Team 2020), running R version 4.2.2 (R Core Team 2021).

Results

Overall, Hemiptera (true bugs, aphids, scale insects, plant- and leafhoppers, cicadas, bed bugs), Hymenoptera (wasps, bees, ants, sawflies), Thysanoptera (thrips), Psocodea (bark-, book- and parasitic lice) and Blattodea (cockroaches, termites) are over-represented (above the grey area in Fig. 1A) among the non-native assemblage, while Coleoptera (beetles), Lepidoptera (moths, butterflies), Diptera (true flies, mosquitos, gnats) and Orthoptera (grasshoppers, locusts, crickets, katydids) are under-represented (below the grey area in Fig. 1A). Despite being under-represented, Coleoptera is the most species-rich insect order within both the global insect fauna (40.2%) and among non-native species (29.4%; Table A1). In contrast, Hemiptera represent a much larger proportion of non-native insects (23.5%) compared to the global insect fauna (9.8%), as is the case for Psocodea (1.6% versus 0.6%) and especially Thysanoptera (thrips) (3.6% versus 0.6%; Table A1). Thysanoptera are also the insect order with the largest proportion of non-native species, with 4.2% of their globally described species also occurring as non-native species in at least one of the 12 investigated world regions, followed by Psocodea (1.9%), Hemiptera (1.7%) and Mantodea (praying mantises; 1.7%) (Table A1).

Comparing numbers of non-native species with global species in different trophic groups shows a complex pattern of over- and under-represented groups (Fig. 1B). Among herbivores, Diptera, Hemiptera, Hymenoptera and Thysanoptera are over-represented, while Lepidoptera and Orthoptera are under-represented. Predators among insect orders are generally under-represented (Coleoptera, Diptera, Orthoptera), and Hemiptera, Mantodea and Neuroptera (lacewings, antlions, mantidflies) are within the bounds of expected proportions. Among detritivores, Blattodea and Thysanoptera are over-represented, and Coleoptera, Hemiptera and

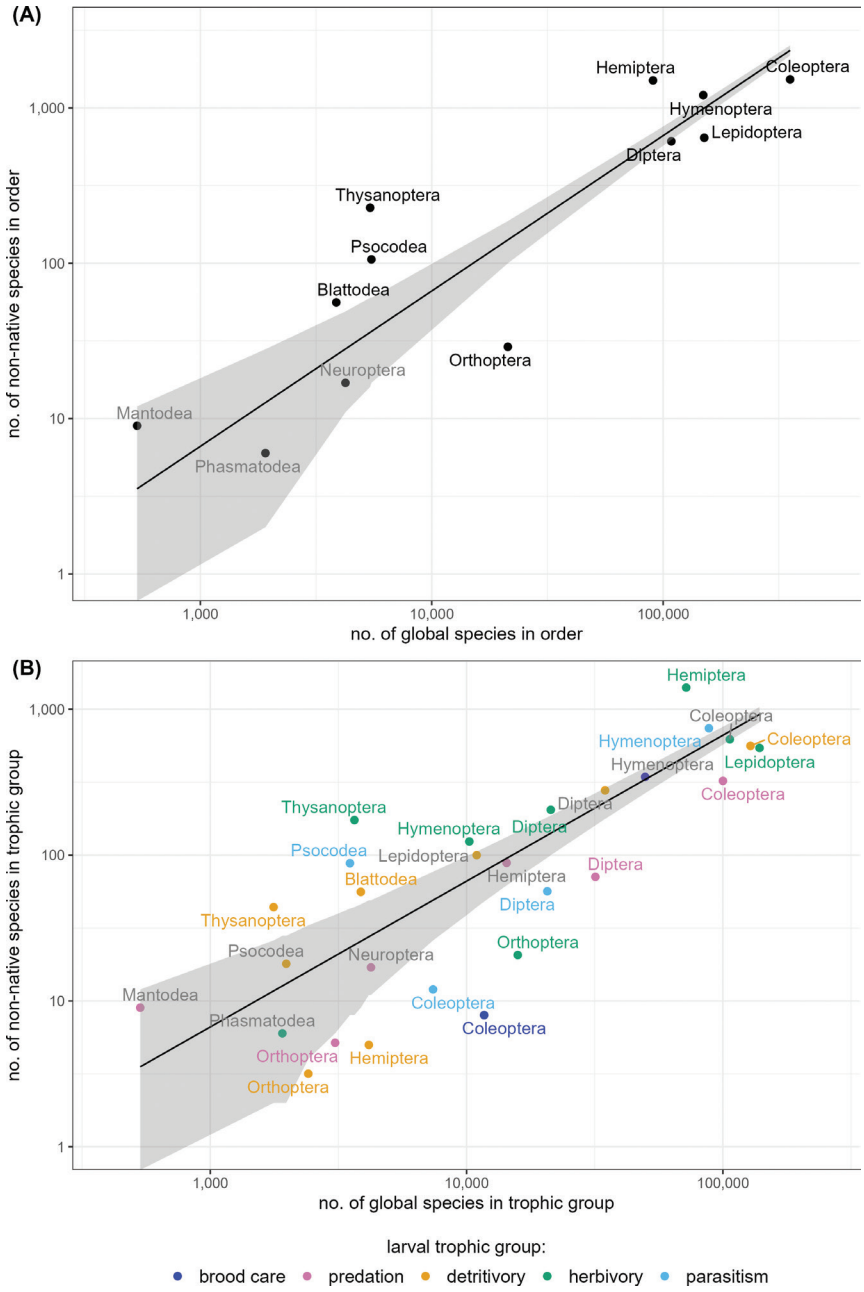

Figure 1. Numbers of non-native species vs. global species **A** per insect order and **B** per larval trophic group (LTG) within each insect order. The black line describes the expected numbers of non-native species per LTG in a given order if in the same proportions as in the globally described species; grey shading indicates the $\alpha = 0.01$ level (under a binomial distribution and with a Bonferroni correction to account for the number of orders compared), with orders outside of this area considered over-represented (above the grey area) or under-represented (below the grey area), and coloured according to their LTG in (B). Order labels in grey indicate trophic groups of insect orders that are within the expected range of proportions. Colours of dots indicate LTG.

Orthoptera under-represented. Among parasites, Hymenoptera and Psocodea are over-represented, whereas Coleoptera and Diptera are significantly below the expected proportion of non-native species to global species. Among brood carers, Coleoptera are under-represented, while Hymenoptera are within the bounds of expected proportions.

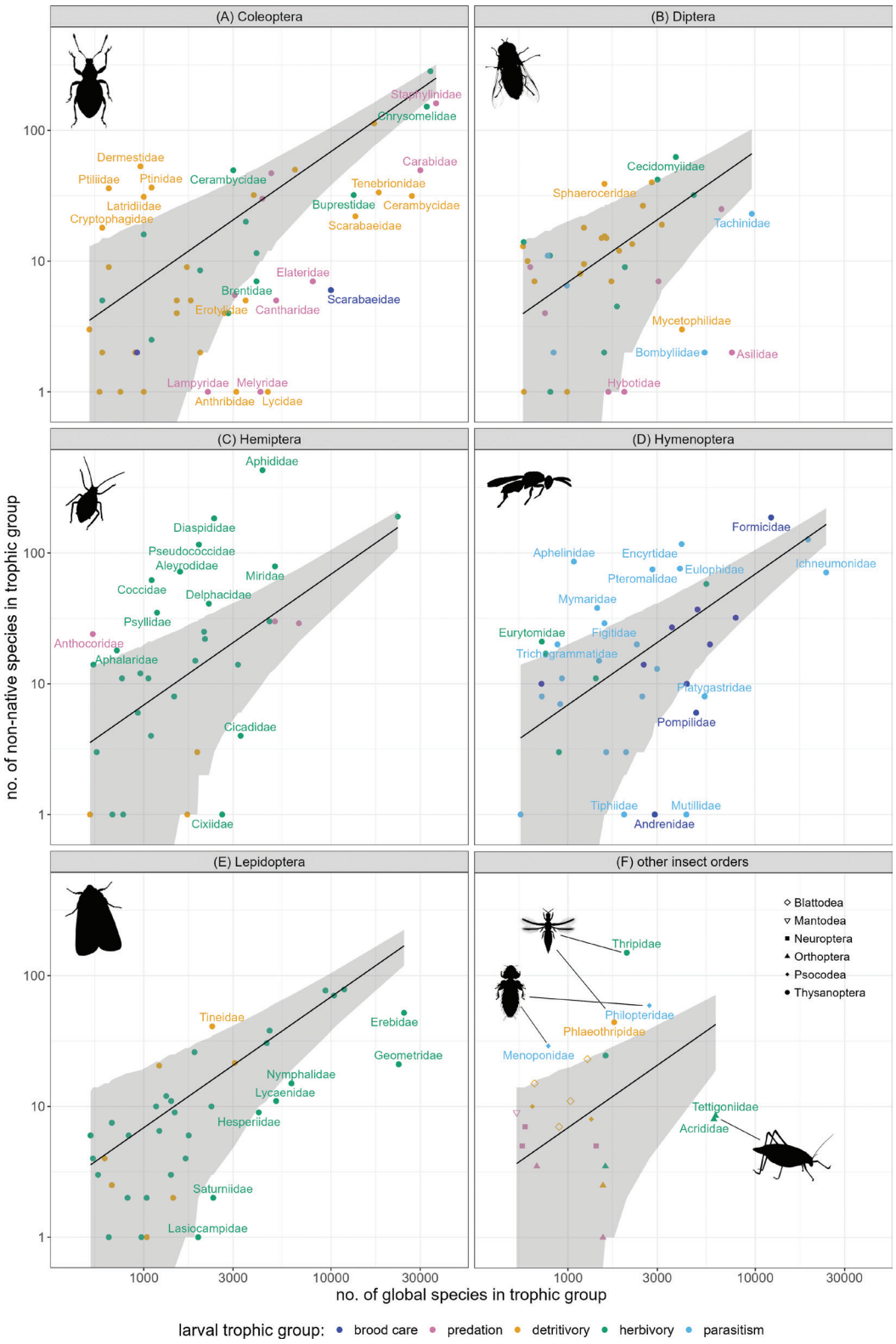

Figure 2. Numbers of non-native species per family–larval trophic group (LTG) combination versus numbers of global species per family–LTG combination for **A** Coleoptera (beetles) **B** Diptera (true flies, mosquitos, gnats) **C** Hemiptera (true bugs, aphids, scale insects, plant- and leafhoppers, cicadas, bed bugs) **D** Hymenoptera (wasps, bees, ants, sawflies) **E** Lepidoptera (moths, butterflies) and **F** the seven less species-rich insect orders. Multi-group families may appear more than once in a panel. The black line describes the expected numbers of non-native species per family if they are in the same proportions as in the globally described species; grey shading indicates the $\alpha = 0.01$ level (under a binomial distribution and with a Bonferroni correction to account for the number of families compared), with labelled families outside of this area considered over-represented (above the grey area) or under-represented (below the grey area).

Among Coleoptera families (Fig. 2A), most of the groups outside the expected proportions are detritivores, with five families over- and six families under-represented. Three herbivorous families are under-represented, whereas only one family is over-represented among non-native herbivores. Among predators, six families are under-represented, as is one family with food-provisioned larvae (brood carers). In the Diptera (Fig. 2B), we find two families over-represented among non-natives (one herbivorous, the other detritivorous), and five families under-represented (two families of each carnivores and parasites, and one family of detritivores). Hemiptera (Fig. 2C) are largely herbivorous, with nine families over- and two under-represented; in addition, one family with predatory larvae is over-represented. Hymenoptera (Fig. 2D) are dominated by parasites, with seven families over- and four under-represented. Furthermore, one family each for herbivores and brood carers is over-represented, and two brood-caring families are under-represented. Among the predominantly herbivorous Lepidoptera, we find seven families under-represented; one family of detritivores is over-represented. In the relatively small order Orthoptera, two herbivorous families are under-represented among non-natives, whereas Psocodea feature two parasitic families over-represented; among Thysanoptera, the detritivorous portion of Phlaeothripidae and the herbivorous Thripidae are above the proportion expected from their global species numbers (Fig. 2F).

After accounting for trophic group, certain insect orders had significantly more non-native species (relative to the global species average) than others (Table A2). Among herbivores, families belonging to Hemiptera and Thysanoptera were more over-represented in non-native assemblages (based on their estimated marginal means), while families in Coleoptera, Lepidoptera and Polyneoptera were more under-represented (Fig. 3A). Among parasites and brood carers, families belonging to Hymenoptera were more over-represented in non-native assemblages (Fig. 3D, E), whereas families in Diptera were more under-represented among parasites (Fig. 3D), and families in Coleoptera were more under-represented among brood carers (Fig. 3E). Among detritivores and predators (Fig. 3B,C), no significant differences were found between orders.

Analysis of historical composition of invasions from 1850 to 2009 indicate that the proportions of beetles (Coleoptera) significantly decreased over time in all occupied larval trophic groups, as was the case for Orthoptera (Fig. 4F). Proportions of thrips (Thysanoptera), on the other hand, significantly increased over time among herbivores, detritivores and predators. Psocodea significantly increased over time among detritivores (although only making up a small fraction), and significantly decreased among parasites. Hymenoptera significantly increased over time both among parasitic and food-provisioned larvae.

Over the course of 16 decades (1850s to 2000s), all of the six largest insect orders experienced a significant upward trend in herbivore invasion rates (Fig. 5, Table A4). Invasion rates of detritivores significantly increased for Thysanoptera (Fig. 5F), Coleoptera and Diptera, and in the latter two orders at times exceeded the invasion rates of herbivores (Fig. 5A, B). Predator invasion rates increased over time in Hemiptera, whereas in Coleoptera and Diptera, no trend was found (Table A4). Invasion rates of parasites significantly increased in Diptera (Fig. 4B), and even more so in Hymenoptera (Fig. 5D). The rate of invasions of brood carers steadily increased in the Hymenoptera (Fig. 5D), but not in the Coleoptera (Fig. 5A).

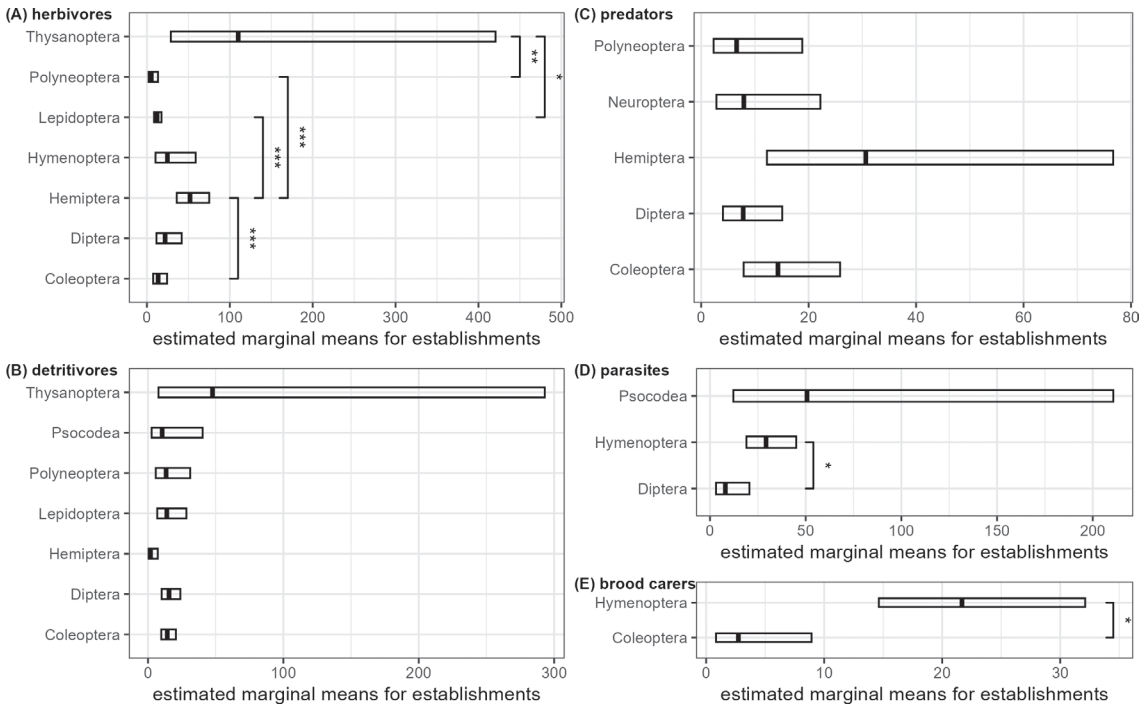

Figure 3. Comparison of estimated number of non-native species per family as a function of numbers of global species in the same family, between orders within each larval trophic group **A** herbivores **B** detritivores **C** predators **D** parasites, and **E** brood carers. Asterisks indicate levels of significant differences between pairs of orders: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

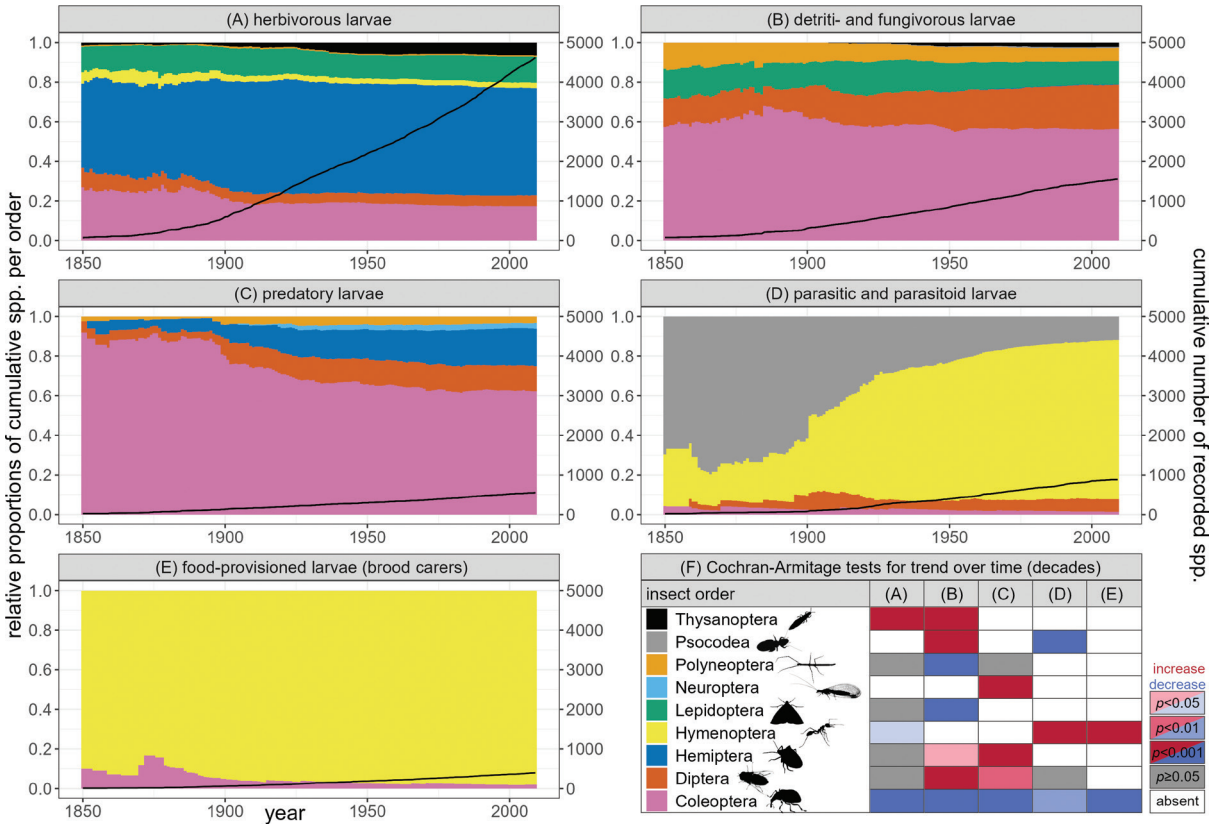

Figure 4. Relative proportions of insect orders (number of accumulated non-native species; left y-axis) over time for **A** herbivores **B** detritivores **C** predators **D** parasites and **E** brood carers. Black line represents the cumulative number of recorded non-native species in each feeding group (right y-axis) **F** the heatmap indicates orders with significant increases (shades of red) or decreases (shades of blue) in proportions of a given trophic guild over time (per decade) based on Cochran-Armitage tests (Table A3).

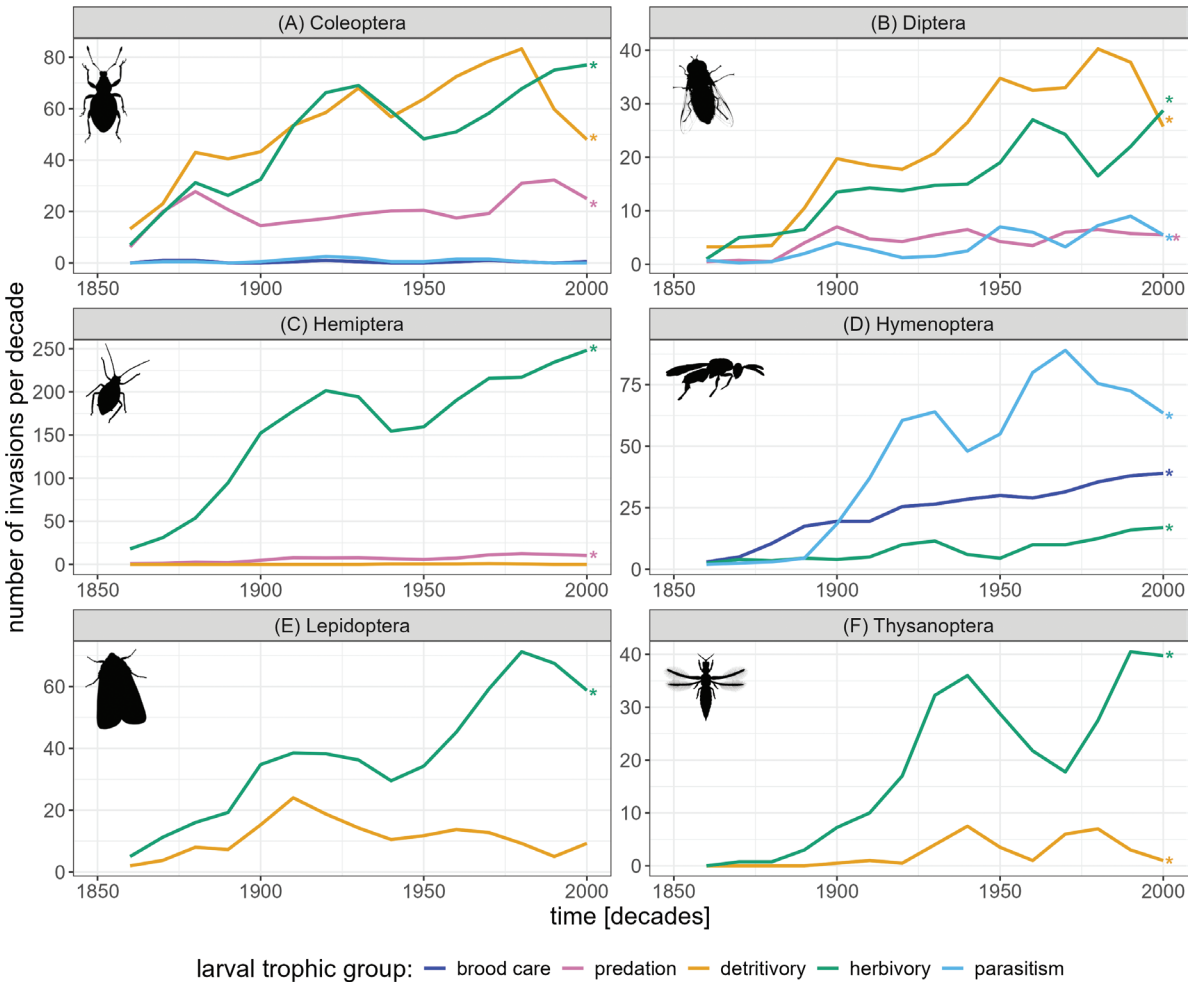

Figure 5. Insect invasion rates: moving averages (20-year moving window) of newly recorded non-native species per decade (1850s to 2000s) in any of the 12 investigated world regions, in different larval trophic groups of **A** Coleoptera **B** Diptera **C** Hemiptera **D** Hymenoptera **E** Lepidoptera, and **F** Thysanoptera. An asterisk (*) at the right end of a curve indicates a significant ($p < 0.05$) upward trend (i.e., increased invasion rate) over time based on Mann-Kendall tests (Table A4).

Discussion

Our first hypothesis — that taxa with predominantly herbivorous larvae are generally over-represented among non-native species — was verified for some orders, but not others: while Hemiptera and Thysanoptera are strongly over-represented among non-native insects, Lepidoptera and Orthoptera are under-represented (Fig. 1A). We find a very similar pattern for the herbivore proportions among orders, with both Hemiptera and Thysanoptera being over-, and Lepidoptera and Orthoptera under-represented (Fig. 1B). A more fine-grained picture emerges when orders are broken up into families. Within Hemiptera, we find nine families over-represented, namely Sternorrhyncha (aphids, scale insects, whiteflies) with Aleyrodidae, Aphalaridae, Aphididae, Coccidae, Diaspididae, Pseudococcidae and Psyllidae, Auchenorrhyncha (cicadas, spittlebugs, leaf-, tree-, planthoppers) with Delphacidae, and Heteroptera (true bugs) with Miridae (Fig. 2C). Among Lepidoptera, three families of butterflies (Hesperiidae, Lycaenidae, Nymphalidae) and four families of macromoths (Erebidae, Geometridae, Lasiocampidae and Saturniidae) are under-represented (Fig. 2E), making this insect order a key exception to the general trend of herbivores being successful invaders.

Our second hypothesis, stating that after accounting for trophic group, non-native species in all orders and families are equally represented relative to their global composition, was not found to be true. Within trophic groups, species in families belonging to certain orders were more over-represented than others. These trends appeared strongest for herbivores; families belonging to the Hemiptera and Thysanoptera were more over-represented in non-native assemblages, and families in the Coleoptera, Lepidoptera and Polyneoptera were more under-represented (Fig. 3A).

Conclusions for these two hypotheses indicate that invasion success is not only determined by the trophic role of a group, but also by other traits. It is possible that species in certain taxa are strongly associated with specific pathways and this leads them to be more commonly transported than other taxa. It is worth noting that among the over-represented orders, most families of Hemiptera and Thysanoptera are sap-feeding herbivorous insects that are commonly associated with imported plants (Moritz 2006; Liebhold et al. 2012; Roques et al. 2020; Fenn-Moltu et al. 2023). Liebhold et al. (2024) observed that the over-representation of Hemiptera among non-native species worldwide is largely driven by over-representation of species in the Sternorrhyncha, potentially explained by the dominance of asexual reproduction in addition to the historical association of these species with plant imports. Similarly, Thysanoptera primarily engage in parthenogenetic reproduction (Moritz 2006), identifying parthenogenesis as a potential key trait for invasion success, especially since it is also expected to reduce Allee effects (Drake 2004). Size also appears to play a role in invasion success among herbivores, with many of the over-represented families consisting of species with a generally small body size (most Hemiptera families, Cecidomyiidae in Diptera, Eurytomidae in Hymenoptera), while the under-represented herbivore families in Lepidoptera and Orthoptera comprise species of relatively large size.

Our third hypothesis is that fractions of non-native species in different orders and trophic groups have not varied historically over time. While the relative distribution of non-native herbivores among orders has largely remained constant over the last 150 years (Fig. 4A), there has been a drastic shift among parasites (Fig. 4D); proportions of Psocodea have dropped while proportions of Hymenoptera have increased. The non-native parasitic Psocodea in our dataset are ectoparasites of birds, and widespread intentional introductions of bird species in many world regions (Dyer et al. 2017) created pathways and niches that favoured Psocodea species establishment. Meanwhile, strong increases in numbers of insect herbivore invasions (Fig. 5) created niches for insect parasitoids that use these herbivores as hosts, thereby facilitating their invasions.

Classic stored product pest groups are over-represented among detritivores: cockroaches (Blattodea) (Fig. 1B), Dermestidae, Ptiliidae and Ptinidae, as well as the more fungivorous Cryptophagidae, Latridiidae and Silvanidae among Coleoptera (Fig. 2A), and Tineidae (clothes moths) among Lepidoptera (Fig. 2E). Probably due to their generalist diet, and close association with human foodstuffs, many species in these families established historically early and are nowadays found in numerous world regions (Bertelsmeier et al. 2025). Similarly, the relatively general larval diet of Sphaeroceridae (Fig. 2D) would give them an advantage as invaders. Thrips, irrespective of their trophic group, are generally closely associated with plants (Sabelis and van Rijn 1997; Moritz 2006), which may explain the over-representation of Phlaeothripidae (Fig. 2F). Fungivory, on the other hand, may limit invasion success and could explain the under-representation of several families, such as the Mycetophilidae (Søli 2017) (Fig. 2D), Anthribidae (Holloway

1982) and Erotylidae (Leschen and Buckley 2007) (Fig. 2A). The role of fungivory among non-native insects is a topic of future research given that the precise larval food source remains unclear for numerous insects and is difficult to discern from larval associations with certain substrates such as rotting wood.

Predators are generally under-represented among non-native insects (Figs 1B, 2), and only the family Anthocoridae (minute pirate bugs) is found over-represented (Fig. 2C). The success of anthocorids might be attributable to their close association with plants, where they often inhabit cryptic habitats (Lattin 1999). Although Coleoptera are still proportionally the largest group among non-native predators, their share has significantly decreased over time, while the proportion of Diptera, Hemiptera and Neuroptera significantly increased (Fig. 4F). Although historically, predation played a larger role, this group is nowadays significantly smaller compared to the estimated global proportion of insect predators (Mally et al. 2024). Changes in invasion pathways over time and improved biosecurity measures might explain the generally low invasion success among predators.

Non-native insects with parasitic larvae are dominated by Hymenoptera and Psocodea, with both groups over-represented at the order- (Fig. 1B) and family-level (Fig. 2D,F). Among Psocodea, the families Menoponidae and Philopteridae, whose species are bird ectoparasites, are over-represented (Fig. 2F). Parasitic Psocodea invasions were predominant in the second half of the 19th century (Fig. 4D), correlating well with the first wave of non-native bird introductions on a global scale (Dyer et al. 2017). A strongly increasing invasion rate of parasitic Hymenoptera at the beginning of the 20th century (Fig. 5D) drastically shifted proportions among non-native parasites, with Hymenoptera now being the largest order (Fig. 4D). Despite their strong decrease over time, non-native parasitic Psocodea are still over-represented on a global scale (Fig. 1B).

There is substantial invasion disharmony among parasitic Hymenoptera, with many families being over-represented (Fig. 2D). The broad host spectrum of Mymaridae (fairyflies), Trichogrammatidae and Eulophidae, and the latter family's diverse forms of host interaction (Gauthier et al. 2000), might have contributed to their invasion success. The invasion success of several other families may be tied to the invasion success of their hosts: Figitidae primarily parasitise the section Schizophora among Diptera (Buffington et al. 2007), such as the over-represented Sphaeroceridae (Fig. 2B). Aphelinidae and Encyrtidae are primarily parasitoids of Hemiptera (Hayat 1983, Noyes 1988), and their invasion success may at least in part rely on the strong invasion success of their hosts (Fig. 2C). Some species of Eulophidae are parasites of thrips (Loomans and van Lenteren 1995), and the invasion success of Thysanoptera (Fig. 2F) may have contributed to their over-representation among non-native insects. Large numbers of parasitoids have been unintentionally introduced in different world regions (Weber et al. 2021), leading to substantial "accidental biocontrol" (Fenn-Moltu et al. 2024), i.e., unintentional pest control through introduced parasitoids. Mally et al. (2024) found zero lag time between invasions of insect herbivores and parasites, surmising that parasitoids may largely be co-introduced along with their insect hosts. Here, we find a decrease in the invasion rate of parasitic Hymenoptera in the 1930s to 1950s (Fig. 5D) that coincides with a contemporaneous decrease among invasions of herbivorous Coleoptera, Hemiptera and Lepidoptera (Fig. 5A, C, E). The fact that a similar dip in invasion rates in that time window is absent in other trophic groups adds further support to the hypothesis of insect herbivores facilitating the introduction of their parasitoids.

The proportion of brood carers among Coleoptera are under-represented (Fig. 1B), which can be attributed especially to Scarabaeidae (Fig. 2A). Many scarabaeid species rely on dung as larval food, with the parents preparing collected dung into a brood structure. The negligible representation of dung among invasion pathways, at least nowadays, may explain the under-representation of scarabeids. Among brood-caring Hymenoptera, Formicidae (ants) are over-represented, whereas Andrenidae and Pompilidae are under-represented (Fig. 2D). The key difference in their invasion success may lie in the degree of sociality: ants are eusocial and form socially complex colonies, whereas the under-represented families are solitary brood carers. Brood-caring insects represent only 5.9% of non-native insects in nine world regions, a significantly smaller proportion than among global insect species (Mally et al. 2024), yet they range among the most impactful biological invaders (Holway et al. 2002; Rabitsch 2011; Bertelsmeier et al. 2017). Eusociality is characterised by individuals living in large colonies with two or more overlapping generations of individuals divided into reproductive and non-reproductive castes, and engagement in cooperative care for the young (Wilson and Hölldobler 2005). Eusociality is thus argued to be responsible for the high invasiveness of many of these insects due to their "social immunity" and "superorganism resilience", to collective foraging, and to mating systems and breeding structures (Moller 1996; Ugelvig and Cremer 2012; Straub et al. 2015; Eyer and Vargo 2021). In addition, ants contain a number of non-native "tramp species" that are strongly tied to human activities (Passera 1994), further attributing to their success as invaders.

There is a general paucity of detailed information on larval feeding modes for the majority of insect species in the world. We therefore extrapolated estimates of feeding group proportions for families with more than one major trophic group based on what is described in the literature. Naturally, with some groups of insects being better investigated than others, the accuracy of these estimates varies. This taxonomic bias, with well-studied charismatic groups like beetles, butterflies and bees versus groups like Diptera and parasitic Hymenoptera, which likely still comprise (ten/hundred) thousands of undescribed species (Miraldo et al. 2024), adds further uncertainty. Species in poorly studied groups are also more likely to remain unidentified at the species-level and thus will not show up in our data. Moreover, we recognise a reporting bias linked to search effort: while certain (often large-bodied) species are easily collected, the increased search effort associated with subterranean species (root- and detritus-feeders, predators in soil), borers living under bark and in plant tissue such as wood and fruits, and parasitoids whose detection requires rearing from their hosts renders such organisms potentially under-reported. Lastly, lists, especially of parasitic insect groups such as Hymenoptera and Diptera, may contain errors because we may have failed to exclude some species that were actually intentionally introduced (e.g. for biocontrol purposes). Also, a large fraction of parasitic species may be incompletely described and there is uncertainty about their native ranges.

Conclusions

Insects in certain orders and families are more likely to invade regions outside of their native range. Overall, herbivorous insects are over-represented among non-native species, but that pattern varies considerably among insect orders and families. The global proliferation of non-native plants creates niches that facilitate invasions of herbivorous insects (Bertelsmeier et al. 2024), but among herbivorous

insects and within other trophic groups, species in certain orders or families are more or less likely to invade. Species within such taxa may share similarities in their biology that either facilitate their transport, e.g., the association of wood-boring insects with wood packaging material in trade (Brockerhoff et al. 2006), or affect their ability to establish following transport, e.g., asexually reproducing species, which may be more likely to establish from small founding populations. Within each trophic group, proportions of invading species in different orders have remained relatively constant over time, though there are a few exceptions, such as the growing representation of Hymenoptera among parasites. This trend likely reflects the niches created for parasitoids as non-native herbivorous insects continue to establish. These results provide useful information for efforts to characterise the risk of insect invasions in the future.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Appendix 1

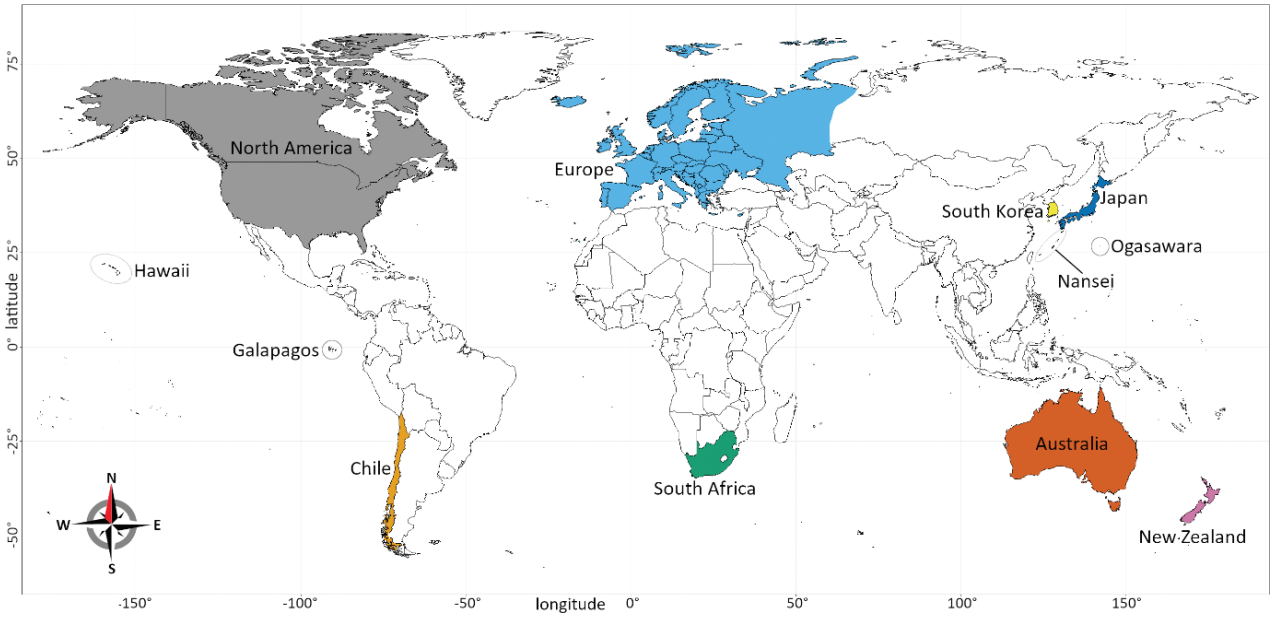

Figure A1. World map illustrating the 12 regions from where lists of non-native insect species were used.

Table A1. Global and non-native numbers of species in different insect orders. Numbers of global species are the sums of families with at least 500 species in a given order. Non-native species are unique species (without duplicates present in more than one world region) pooled among the 12 investigated world regions.

Insect order	Number of global spp.; = A	Proportion [%] of global spp. in order among total global insect spp.; = (A/ΣA)*100	Number of non-native spp.; = B	Proportion [%] of non-native spp. among total non-native spp.; = (B/ΣB)*100	Proportion [%] of non-native spp. among global spp. in the insect order; = (B/A)*100
Blattodea	5,782	0.64	56	0.86	0.97
Coleoptera	363,663	40.18	1,925	29.43	0.53
Diptera	108,486	11.99	664	10.15	0.61
Hemiptera	88,511	9.78	1,534	23.46	1.73
Hymenoptera	148,951	16.46	1,237	18.91	0.83
Lepidoptera	150,561	16.64	687	10.50	0.46
Mantodea	533	0.06	9	0.14	1.69
Neuroptera	4,237	0.47	17	0.26	0.40
Orthoptera	21,321	2.36	63	0.96	0.30
Phasmatodea	1,911	0.21	6	0.09	0.31
Psocodea	5,486	0.61	106	1.62	1.93
Thysanoptera	5,594	0.62	236	3.61	4.22
SUM	905,036	100	6,540	100	–

Table A2. Pairwise ratios of estimated marginal means of negative binomial generalised linear models. Asterisks indicate levels of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

HERBIVORES	**Diptera**	**Hemiptera**	**Hymenoptera**	**Lepidoptera**	**Neuroptera**	**Polyneoptera**	**Psocodea**	**Thysanoptera**
Coleoptera	0.616	0.260**	0.547	1.099		2.569		0.123
Diptera		0.421	0.888	1.783		4.170		0.199
Hemiptera			2.106	4.229***		9.889***		0.472
Hymenoptera				2.008		4.696		0.224
Lepidoptera						2.338		0.117*
Polyneoptera								0.048**
DETRITIVORES	**Diptera**	**Hemiptera**		**Lepidoptera**		**Polyneoptera**	**Psocodea**	**Thysanoptera**
Coleoptera	0.916	7.709		1.023		1.064	1.361	0.298
Diptera		8.418		1.117		1.162	1.486	0.326
Hemiptera				0.133		0.138	0.177	0.039
Lepidoptera						1.040	1.331	0.292
Polyneoptera							1.280	0.281
Psocodea								0.219
PREDATORS	**Diptera**	**Hemiptera**			**Neuroptera**	**Polyneoptera**		
Coleoptera	1.828	0.466			1.799	2.167		
Diptera		0.255			0.984	1.185		
Hemiptera					3.858	4.646		
Neuroptera						1.204		
PARASITES			**Hymenoptera**				**Psocodea**	
Diptera			0.274*				0.158	
Hymenoptera							0.578	
BROOD CARERS			**Hymenoptera**					
Coleoptera			0.126**					

Table A3. Cochran-Armitage tests for trend over time (decades from 1850 to 2009) for the five larval trophic groups (LTGs); dim = 16 and alternative hypothesis = one-sided for all comparisons. Positive Z values indicate increase over time, negative Z values decrease over time. Asterisks indicate levels of significance: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$. This table corresponds to the heatmap shown in Fig. 4F.

Comparison order vs. Σ(other orders)	**Herbivores**	**Detritivores**	**Predators**	**Parasites**	**Brood carers**
Coleoptera	Z = -5.4219***	Z = -3.1342***	Z = -7.9353***	Z = -2.4746**	Z = -3.4309***
Diptera	Z = -0.2362	Z = 7.6545***	Z = 2.906**	Z = 1.0312	
Hemiptera	Z = 0.08353	Z = 2.3031*	Z = 6.2854***		
Hymenoptera	Z = -1.9008*			Z = 19.832***	Z = 3.4309***
Lepidoptera	Z = 0.5290	Z = -3.8199***			
Neuroptera			Z = 3.2124***		
Polyneoptera	Z = -0.5578	Z = -4.8094***	Z = 0.2624		
Psocodea		Z = 3.0994***		Z = -21.912***	
Thysanoptera	Z = 10.124***	Z = 6.1885***			

Table A4. Results (tau) of Mann-Kendall tests for monotonic trend over time for each trophic group of each insect order. Asterisks indicate levels of significance: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$.

Tau	**Herbivores**	**Detritivores**	**Predators**	**Parasites**	**Brood Carers**
Coleoptera	0.714***	0.657***	0.410*	0.011	-0.023
Diptera	0.867***	0.766***	0.418*	0.638**	
Hemiptera	0.829***	0.425	0.689***		
Hymenoptera	0.781***			0.733***	0.976***
Lepidoptera	0.714***	0.057			
Thysanoptera	0.746***	0.571**			

Supplementary material 1

World insect families with larval trophic groups

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: Insect families (3rd column) with at least 500 world species with their order (1st column; 2nd column "order_alt" with Blattodea, Mantodea, Orthoptera and Phasmatodea pooled into Polyneoptera), their world species (4th column), estimated world species numbers of larval detritivores (5th column), herbivores (6th column), predators (7th column), parasites (8th column) and food-provided larvae (brood carer species; 9th column); the "references" (10th) column provides citations for the world species numbers and the sources for the estimates of trophic group species numbers. Family names were matched against the GBIF backbone (GBIF 2021), with the following exceptions: in Hymenoptera, Figitidae incl. Eucoilidae, Vespidae incl. Eumenidae; in Coleoptera, Ptinidae incl. Anobiidae, Curculionidae incl. Brachyceridae and Dryophthoridae, Scarabaeidae incl. Aegialiidae, Aphodiidae and Cetoniidae, Brentidae incl. Apionidae, Chrysomelidae incl. Bruchidae, Erotylidae incl. Languriidae, Melyridae incl. Malachiidae; in Lepidoptera, Lypusidae incl. Chimabachidae, Erebidae incl. Arctiidae and Lymantriidae, Elachistidae incl. Agonoxenidae, Depressariidae incl. Peleopodidae; in Siphonaptera, Hectopsyllidae instead of the former Tungidae.

Link: https://doi.org/10.3897/neobiota.99.151227.suppl1

Supplementary material 2

Families of non-native insects with larval trophic groups

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: Non-native species pooled to families (3rd column) with their order (1st column; 2nd column "order_alt" with Blattodea, Mantodea, Orthoptera and Phasmatodea pooled into Polyneoptera), summed species numbers of larval detritivores (4th column), herbivores (5th column), predators (6th column), parasites (7th column), food-provided larvae (brood carer species; 8th column), species with unknown larval trophic group (9th column), and sum of all non-native species per family (10th column).

Link: https://doi.org/10.3897/neobiota.99.151227.suppl2

Supplementary material 3

Data for Fig. 1

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: Containing insect orders (1st column) with their larval trophic groups (4th column) and their numbers of global species (2nd column) as well as non-native species (3rd column) per larval trophic group.

Link: https://doi.org/10.3897/neobiota.99.151227.suppl3

Supplementary material 4

Data for Fig. 4

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: Comprising cumulative numbers of non-native species over time (years 1850–2009, including species reported pre-1850), pooled among all 12 investigated world regions, for each order–LTG (larval trophic group) combination. HERBI = herbivores, DETRI = detritivores, CARNI = predators, PARAS = parasites, BROOD = food provisioners (brood carers).

Link: https://doi.org/10.3897/neobiota.99.151227.suppl4

Supplementary material 5

Data for Fig. 5

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: Comprising numbers of non-native species per decade (1850s–2000s), for each combination of order (1st column) and larval trophic group (2nd column).

Link: https://doi.org/10.3897/neobiota.99.151227.suppl5

Supplementary material 6

R script

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: R file

Explanation note: R script containing the code for the analyses and figures.

Link: https://doi.org/10.3897/neobiota.99.151227.suppl6

Supplementary material 7

List of non-native species with larval trophic groups

Authors: Richard Mally, Rebecca M. Turner, Helen F. Nahrung, Takehiko Yamanaka, Gyda Fenn-Moltu, Cleo Bertelsmeier, Alain Roques, Eckehard G. Brockerhoff, Deepa S. Pureswaran, Andrew M. Liebhold

Data type: txt

Explanation note: List of non-native insect species (4th column) from 11 of the 12 investigated world regions (excluding Australia; 5th column), with order (1st column), family (2nd column), global number of species in family (3rd column), year of first record in the respective region (6th column), larval trophic group (7th column), brief description of feeding (8th column), and source (reference) of larval feeding (9th column). The non-native insect species of Australia are not included as public release of these data is not permitted.

Link: https://doi.org/10.3897/neobiota.99.151227.suppl7