Report

Current Biology

Historical invasion rates vary among insect trophic groups

Highlights

- Herbivores are over-represented among non-native insects worldwide
- Predator and detritivore invasion proportions declined since the 18th century
- Herbivore invasion rates are related to historical lagged plant invasions

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In brief

Among non-native insects, herbivores are over-represented compared to the world fauna, and proportions are increasing. In contrast, non-native detritivores and predators are under-represented, with proportions declining. These results are consistent with a mechanism of plant invasions facilitating insect herbivore invasions via niche creation.

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Historical invasion rates vary among insect trophic groups

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SUMMARY

Globalization has spread thousands of invasive insect species into new world regions,[1–3] causing severe losses in ecosystem services. Previous work proposed that plant invasions facilitate insect invasions through the creation of niches for non-native herbivores.[3–6] Despite the impact of insect invasions, a comprehensive understanding is lacking on how invasion success varies among insect feeding groups. We therefore compiled the predominant larval trophic groups (herbivores, predators, parasites, detritivores, and brood-carers) for 5,839 non-native insect species in nine world regions to compare (1) proportions of species in each group between non-native species and the world's fauna, (2) how invasion success for each trophic group has changed over the last three centuries, and (3) how historical herbivore invasions are related to plant invasions over time and parasite invasions are related to herbivores. We find that herbivores represent a significantly larger proportion (52.4%) among non-native insects compared with the world fauna (38.4%), whereas proportions of non-native detritivores (including fungivores), predators, and brood-carers are significantly lower; parasite proportions do not significantly differ. Predators and detritivores dominated among invasions in the 18th century but subsequently diminished, likely due to changing invasion pathways, whereas proportions of herbivores, parasites, and brood-carers increased over time. We found herbivore invasions to lag 80 years behind plant invasions, whereas parasitoids appear to co-invade with their herbivore hosts. The dominance of herbivores among non-native insects and their strong cross-correlation with plant invasions further strengthens the hypothesis that plant invasions drive the global rise in numbers of non-native insects.

RESULTS AND DISCUSSION

Among the 1,122 global families of insects (with a total of 1,056,700 described species), 218 families contain 500 or more species and have primarily terrestrial larvae, accounting for 905,036 species (Data S1); although these only represent 85.64% of the total world insect species, we will refer to this assemblage as "world insects." These species fall into five larval trophic groups: herbivores (feeding on or inside living land plants, excluding algae), detritivores (feeding on dead and decaying animal and plant material, as well as fungi, lichens, and algae), predators (feeding on freshly killed animal tissue of more than one prey item), parasites (feeding on or inside a single living animal host organism, including parasitoids[7]), and brood-carers (larvae provided with food) (see STAR Methods for more details). Herbivores comprise 347,685 species (38.4% of world insects), detritivores 218,106 spp. (24.1%), predators 144,631 spp. (16.0%), parasites (e.g., parasitoids of other insects, bird lice) 131,239 spp. (14.5%), and brood-carers (such as solitary and social Hymenoptera, certain dung beetles) 63,375 spp. (7.0%) (Table S1).

Among nine investigated world regions (Figure S1), non-native insects comprise a total of 6,408 species (10,275 records) in 197 families of at least 500 species (Data S2). Information on the larval trophic group is available for 5,839 of these species (Data S3): herbivores comprise 3,057 spp. (52.4%), detritivores 1,039 spp. (17.8%), predators 511 spp. (15.1%), parasites 886 spp. (8.8%), and brood-carers 346 spp. (5.9%) (Table S1).

Two-sample z tests for equality of proportions indicate that herbivores make up a significantly larger proportion ($p < 2.2e{-}16$) of non-native species compared with the world insects (Figure 1; Table S1). In contrast, proportions of non-native detritivores ($p < 2.2e{-}16$), predators ($p < 2.2e{-}16$), and brood-carers ($p = 0.001408$) each comprise significantly smaller

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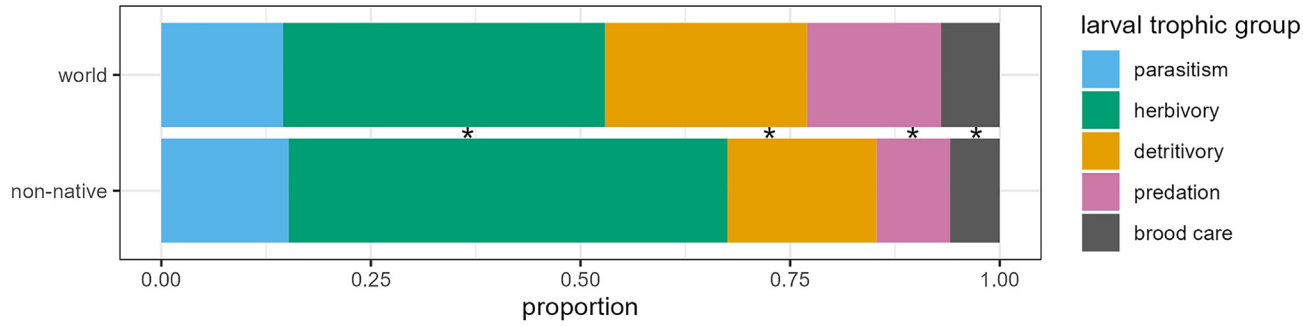

Figure 1. Proportions of species in trophic groups for world and non-native insect assemblages

Estimated proportions of larval trophic groups among world insect species and 5,839 non-native insect species from nine world regions. Asterisks (*) indicate significant differences ($p < 0.05$) between the world and non-native trophic group proportions.
See also Table S1.

proportions among non-native species than among world insects. The proportion of parasites does not significantly differ between world insects and non-native insects ($p = 0.1524$). Over-representation of herbivores and under-representation of detritivores, predators, and brood-carers among non-native insects compared with world species reflects a trend of "invasion disharmony," where the composition of non-native assemblages deviates from native assemblages.[8,9] Invasion disharmony results from the subsetting of species during successive invasion stages (transport, arrival, and establishment), filtering source species pools (described below).

We find substantial changes in the trophic group proportions over the past 300 years. Herbivores were under-represented among non-natives until 1775 but have become by far the largest group among non-native insects since the beginning of the 20th century (Figures 3A and 3B), now comprising more than half of the non-native species (Figure 1; Table S1). During those three centuries, the proportion of herbivores has significantly increased over time (Cochran-Armitage test for trend over time based on 31 decades from 1700 to 2009: $Z = 16.313$, $p < 2.2e{-}16$) (Figure 3H). Over-representation of herbivores may have arisen from two invasion filters. First, there is a long history of accidental introduction of insects with international trade in live plants and plant products.[10,11] The transition of cargo transport from sailing vessels to steamships resulted in shorter transport times,[12,13] facilitating the movement of plant products, which are the primary invasion pathway for herbivorous insects.[10,14] Second, non-native plants are increasingly abundant worldwide through accidental introductions (Figure 2A) and their widespread use in agriculture, forestry, and urban landscapes[15,16]; this plethora of non-native plants creates ecological niches for herbivorous insects, thereby facilitating their invasions.

This is illustrated by our finding of a total of 11,321 plant naturalizations (referred to as plant invasions hereafter) across the nine world regions from 1700 to 2009. The rate of plant invasions steeply increased from the late 18th century to the mid-19th century and plateaued after 1850 to a level of about 1,000 species per decade (Figure 2A). By contrast, there has been a trend of steeply rising invasion rates of herbivores since 1860 (Figure 2B). Cross-correlation analysis indicates a temporally lagged correlation between the two: the strongest positive cross-correlation between detrended decadal sums of plant invasions and herbivore invasions occurs at an 80-year lag (Figure 2C). This is comparable with previous reports of a 110-year lag between plant and insect invasions,[5] and consistent with the theory that plant invasions facilitate herbivore invasions through niche creation.

A development opposite to that of herbivores is observed in detritivores. During the 18th and in the first half of the 19th century, detritivores were the largest group among non-native species (Figure 3A), and they were over-represented compared with their proportion among world insects (Figure 3B). Their historical dominance was likely due to the prevalence of generalist feeding that is independent of previous invasions of their hosts. This is further supported by many historical records of detritivores hitchhiking on sailing ships and in ship ballast prior to 1900.[17–19] Over time, the trophic group experienced a significant decrease in their proportion ($Z = -16.622$, $p < 2.2e{-}16$) based on Cochrane-Armitage tests (Figure 3H). Since 1925, non-native detritivores are significantly under-represented compared with their proportion among world insects (Figure 3B; Table S2). This decrease in the proportion of detritivores may in part be due to the elimination of soil and rock as maritime ballast, which was largely complete by 1900.[12] However, the decrease may also simply reflect the increasing frequency of invasions by herbivorous insects, and/or an under-reporting of detritivores (and other non-herbivorous species) compared with the generally more impactful herbivores. Detritivores are not necessarily omnivores. Some forms of detritus, such as dung and carcasses, are spatially and temporally unpredictable[20] and may, therefore, limit the establishment success of more specialized groups. Future studies are needed to analyze invasions of detritivores and fungivores separately, as the latter may be more host-specific. However, little is known about the food substrate of many species, and among soil-dwelling organisms, non-native species are still poorly studied.[21] Although they are sometimes transported in the soil of potted plants, which is also a primary pathway for herbivores feeding on plants themselves, their detection might be severely under-reported.

Like detritivores, many insect predators are generalists[22] and have historically "hitchhiked" in rock and stone maritime ballast.[18,23] Similarly, the elimination of this pathway and improved biosecurity limits on the transport of soil may be partially responsible for the proportional decline of predators

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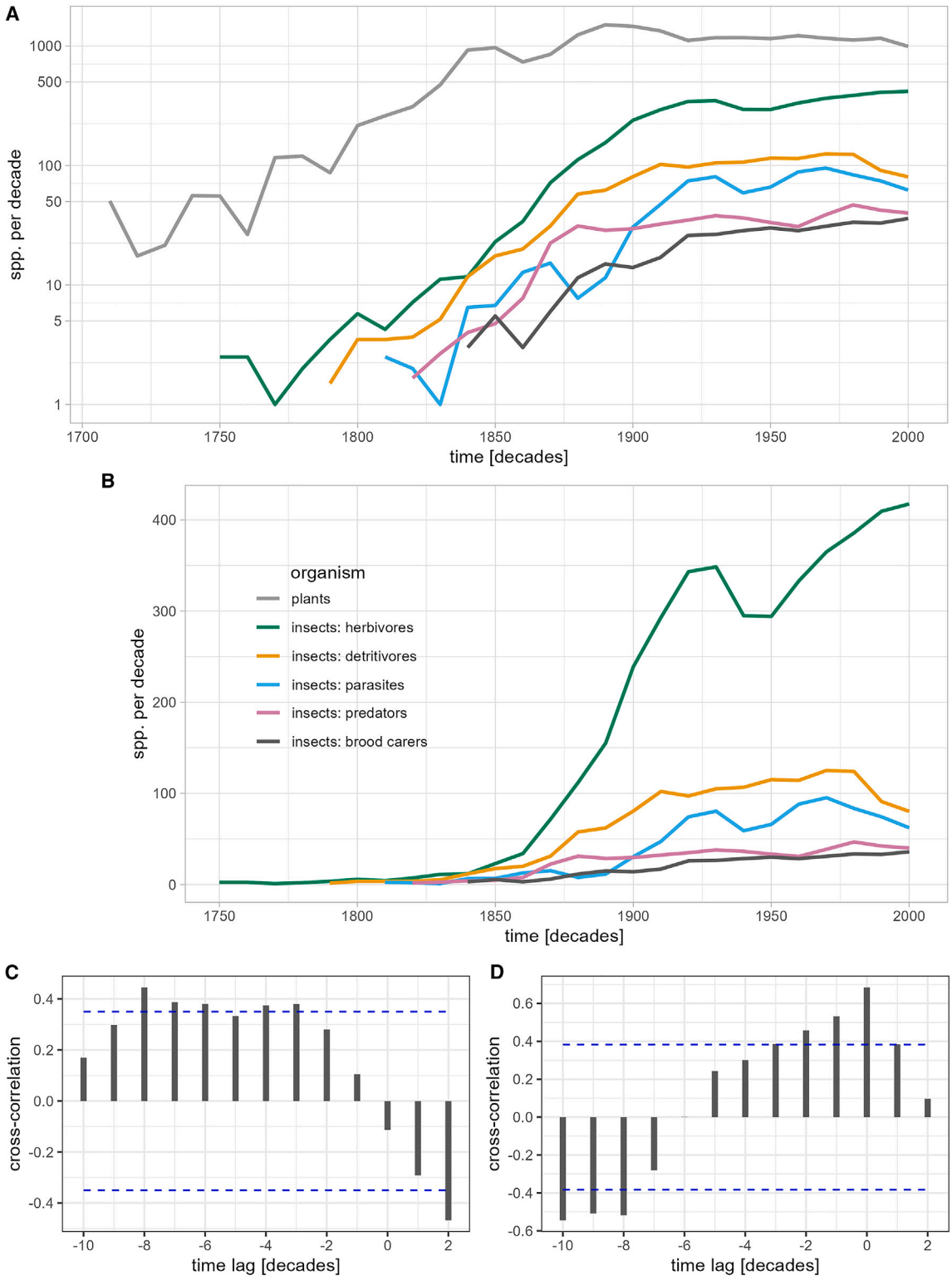

Figure 2. Invasion rates over time

(A and B) Non-native species discovered per decade (based on 20-year moving averages) pooled among nine world regions for (A) plants and the five insect trophic groups from 1700 to 2009, on a $\log_{10}$ scale, and (B) for the five insect trophic groups from 1750 to 2009, on a linear scale.

(C and D) Cross-correlograms of (C) plants vs. herbivores (decades from 1700s to 2000s) and (D) herbivores vs. parasites (decades from 1750s to 2000s), with time lags ranging from −10 decades to +2 decades. For both analyses, the detrended number of species reported per decade from all nine world regions was used, with species reported from more than one world region counted as replicate invasion events. Blue dashed lines indicate critical correlation levels.

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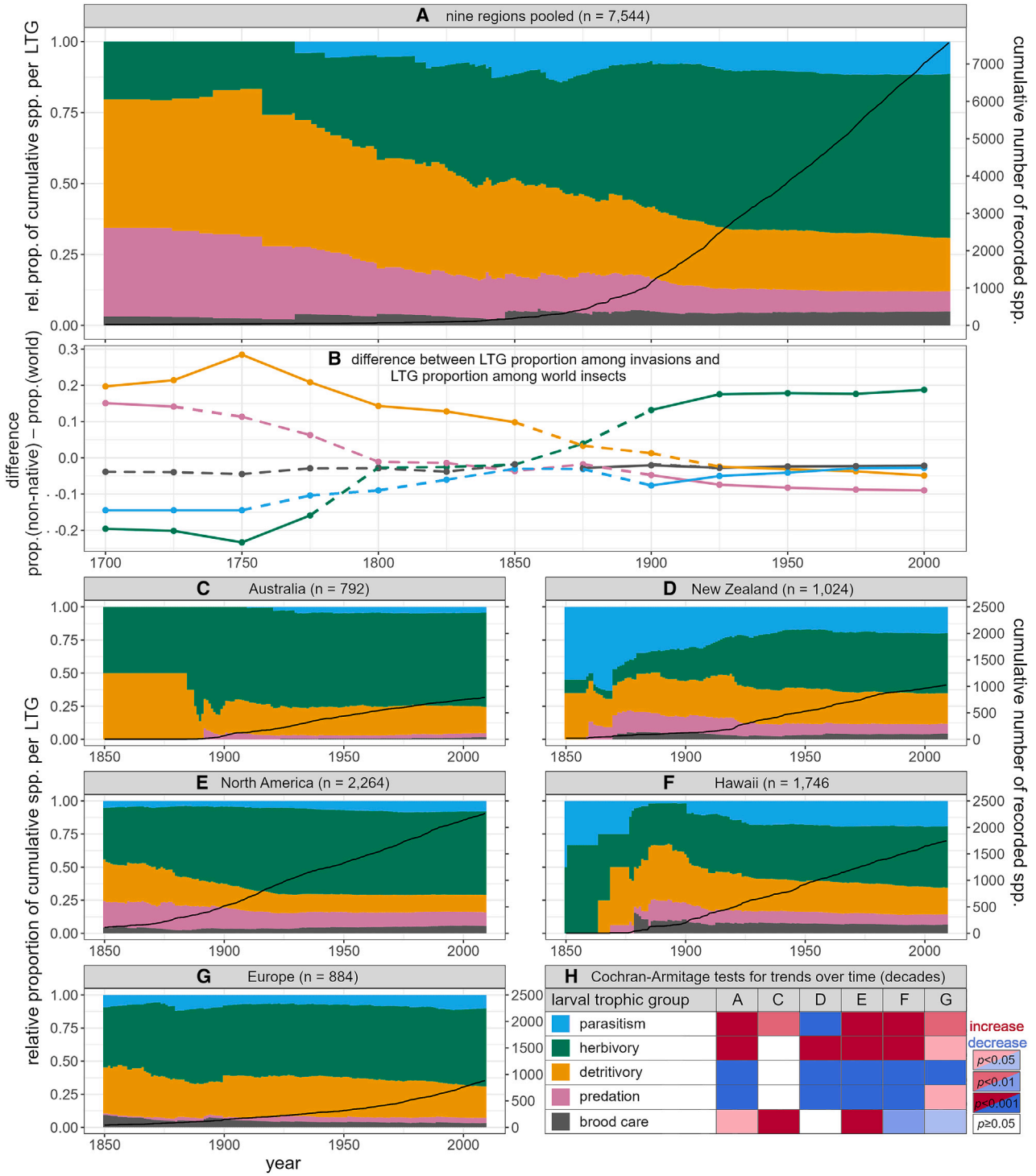

Figure 3. Insect trophic group proportions over time

Relative proportions (left, y axis) of cumulative non-native species in each larval trophic group (LTG) over time (x axis), (A and B) pooled as separate invasion events among the nine investigated world regions (years 1700–2009) and (C–G) in the five investigated world regions with the most non-native insect species (years 1850–2009); black lines represent the cumulative number of recorded non-native species (right, y axis). (B) indicates significant differences (solid lines; based on two-proportion z tests) or non-significant differences (dashed lines) between LTG proportions among cumulative non-native insects (shown in A) and LTG proportions among cumulative world insects (as shown for "world" in Figure 1) at 25-year intervals. The heatmap (H) indicates significant proportional increases (shades of red) or decreases (shades of blue) over time (per decade) in the nine pooled world regions (column "A," 1700s–2000s, i.e., 31 decades) and in the five individual regions (columns "C" to "G," 1850s–2000s, i.e., 16 decades) based on Cochran-Armitage tests.

See also Tables S2 and S3.

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over time (Cochran-Armitage test: $Z = -16.129$, $p < 2.2e{-}16$). It is also possible that their under-representation results from under-reporting of predatory non-natives, as they are, like detritivores, usually considered of little economic concern.

The trophic group of brood-caring is the smallest in our analyses, estimated as a mere 7% of the world species, although among non-native insects we find the proportion of brood-carers to be even lower (5.9%). Over time, the proportion of non-native brood-carers increased (Cochran-Armitage test: $Z = 1.8976$, $p = 0.02888$), although the group was historically always under-represented compared with world insects (Figure 3B). In contrast to their low invasion success, 14 of the 100 world's worst invasive insect species are brood-carers.[24] Their high impact (but not necessarily invasion success) in non-native regions may be attributed to their eusociality[25] and associated traits[26] in combination with a relatively generalist diet, "enemy release" from parasites, and "social immunity."[27]

Although globally the proportion of established non-native parasites does not differ from the world proportion (Figure 1; Table S1), we found an increase of this trophic group over time worldwide (Cochran-Armitage test: $Z = 8.6801$, $p < 2.2e{-}16$) (Figures 3A–3B). Despite this general increase in the global *proportion* of parasites among all non-native insects, the *invasion rate* of parasites declined in the 2nd half of the 20th century (Figure 2B). This may reflect increased intentional release of parasitoids for biological control (intentional introductions were omitted from our analyses), so that fewer niches for the establishment of accidentally introduced parasitoids are available. Interestingly, the opposite is reported for Hawaii, where fewer intentional releases of parasitoids took place in the 1980s and 1990s,[28] a pattern that may be correlated with increasing success in the intentional introduction of parasitoids.[29] Another explanation may be the accumulation of host switches by native generalist parasites to non-native herbivores, preventing specialist parasites from the host's native range to reunite with their host due to pre-emptive occupation of that niche in the invaded range. Our very general treatment of parasites as one trophic group may obscure more complex underlying patterns in their invasion success, requiring a more fine-scaled future analysis of generalist and specialist parasites.[30]

Invasions by herbivores probably create niches for specialist parasitoids that use them as hosts. Investigating temporal lags between herbivore invasions and parasite invasions, we observed the strongest positive cross-correlation at lag zero, i.e., without time lag (Figure 2D). This may be because insect parasitoids (especially parasitic Hymenoptera) are co-introduced with their herbivore hosts. The similar shapes of the invasion rate curves of herbivores and parasites over time, including the drop in the 1930s (Figure 2B), supports this. With parasitoids co-invading with their hosts, herbivores thus appear to experience less natural enemy release than plants.

Whereas previous research has shown steep increases in non-native insects in general,[1,5] our subdivision into trophic groups provides a more nuanced evaluation (Figure 2B). Considering that herbivores contribute 52.4% of non-native insects in our dataset, observed increases in numbers of insect invasions[1,5] appear to be mainly driven by the rise in herbivore numbers. Invasion rates of non-herbivores have stagnated since ~1900, indicating that dynamics of insect invasions do not strictly trace the general dynamics of trade (which has accelerated over the last century). This could be a result of some combination of a depletion of source species pools,[31] changes in invasion pathways,[14,32] and partial success of national and international biosecurity programs that target prevention.[33] For example, Yamanaka et al. found a stronger influence of climate than trade affecting establishment likelihood.[34] Species accumulation curves have attenuated in Australia and New Zealand (Figures 3C and 3D), likely due to strict quarantine measures implemented in the second half of the 20th century, whereas in Europe invasion rates are still rising (Figure 3G). Similar observations exist for arthropods for Australasia and Europe,[35] predicting strong increases in the latter region. It is still not entirely clear why Europe still accumulates non-native insects at such a high rate, but reasons might be the long-standing role of Europe as donor region of non-native plant and insect species[36,37]; the fall of the "Iron Curtain," which may have increased the "invasibility" of Europe[38]; and the comparatively open approach of the European Union for imports of plants for planting.[39]

Our results also agree, in part, with other findings,[40] namely that global insect invasions occurred in two waves, with a decrease in the invasion rate in the first half of the 20th century. Here, we find a decreased invasion rate for herbivores and parasites in the 1930s, but no clear decline for the other three trophic groups. This decrease may have been an effect of the great economic depression or a result of new biosecurity measures implemented in the early 1900s.[33]

Among the five world regions with the most non-native species (Figures 3C–3G), we found a significant increase in proportions of parasites over time, except in New Zealand (Figure 3D), where parasite proportions significantly decreased (Figure 3H; Table S3). This is likely due to a large influx of domestic animals and European birds,[41] along with their parasites, in the second half of the 19th century, followed by a strong increase in the proportions of other feeding groups. Proportions of herbivores significantly increased in most regions, and those of detritivores and predators decreased, except in Europe (Figure 3G), where predator proportions increased over time; no significant trend over time was observed in Australia for herbivores, detritivores, and predators (Figures 3C and 3H). Proportions of brood-caring insects increased in Australia and North America but decreased in Hawaii and Europe.

Information on trends in invasion rates are critical to the development of biosecurity policies worldwide.[42] Although our results provide new insight into the drivers of invasion trends, we acknowledge limitations. Temporal patterns are based on first-occurrence records; actual establishments likely preceded these discoveries by several years,[43–45] so variation in discovery effort through time and across taxa could affect observed temporal patterns. For this reason, we removed first records after 2009 from our analyses, as these showed signs of reporting lag. Although we limited our analysis to regions where comprehensive lists of non-native species were available, we acknowledge that these lists are inevitably incomplete. The tendency of certain groups of non-native insects (e.g., large species) to be more readily noticed[46] may introduce systematic bias in estimates of proportions of species in different trophic groups. Perhaps the over-representation of herbivores is an artifact of them being more likely to be noticed because of their economic impacts.

However, the same bias also likely exists for native species and thereby affects estimates for world assemblages. Also, the fraction of non-native insects that cause noticeable damage is typically small.[47] Furthermore, knowledge about modes of feeding is lacking or incomplete for many insect species in mixed families and can only be inferred from a small body of literature on feeding associations of phylogenetically related species. Our estimates of trophic group proportions for mixed families are likely only approximate in some cases.

Overall, we show that over the course of three centuries there has been a substantial turnover in the proportions of trophic groups among invading insect species, from early domination by detritivores and predators to domination by herbivores in all regions. Given the continual spread of invasive plants and widespread use of non-native plants in agriculture, forestry, and horticulture, it can be anticipated that this pattern of niche creation following plant invasions will continue in the future. Managing the proliferation of non-native plants thus could create an opportunity for biosecurity programs aimed at reducing future insect invasions. Lastly, this study focused on the richness of non-native insects, which is representative of risk from a larger species pool but does not necessarily translate to ecological or economic impact.[48]

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Richard Mally (mally@fld.czu.cz).

Materials availability

This study did not generate new unique materials.

Data and code availability

- The lists of world insect families with at least 500 species, families of non-native species, and non-native species from eight of the nine world regions, each with data on larval trophic group, have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.M.L., R.M., and R.M.T.; methodology, A.M.L., R.M., R.M.T., and T.Y.; formal analysis, R.M. and A.M.L.; data curation, R.M., R.M.T., and H.F.N.; writing – original draft, R.M., R.M.T., H.F.N., T.Y., G.F.M., C.B., and A.M.L.; writing – review & editing, R.M., R.M.T., H.F.N., T.Y., G.F.M., C.B., and A.M.L.; visualization, R.M., T.Y., and G.F.M.; supervision, A.M.L.; project administration, A.M.L.; funding acquisition, A.M.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Data sources for world insect dataset (Data S1)
  - Data sources for non-native insect dataset (Data S3)
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
International Non-native Insect Establishment Data	Turner et al.[49]	DOI
Alien Species First Records Database	Seebens[50]	https://doi.org/10.5281/zenodo.10039630
Global Biodiversity Information Facility taxonomic backbone	GBIF[51]	https://doi.org/10.15468/43g7-9874
insect trait tool	Hörren et al.[52]	https://doi.org/10.1101/2022.01.25.477751
Software and algorithms		
R software	R Core Team[53]	https://www.R-project.org/
R Studio	RStudio Team[54]	http://www.rstudio.com/
broom package	Robinson et al.[55]	https://doi.org/10.32614/CRAN.package.broom
cowplot package	Wilke[56]	https://doi.org/10.32614/CRAN.package.cowplot
data.table package	Barrett et al.[57]	https://r-datatable.com
DescTools package	Signorell[58]	https://doi.org/10.32614/CRAN.package.DescTools
ggh4x package	Van den Brand[59]	https://doi.org/10.32614/CRAN.package.ggh4x
ggplotify package	Yu[60]	https://doi.org/10.32614/CRAN.package.ggplotify
ggpubr package	Kassambara[61]	https://doi.org/10.32614/CRAN.package.ggpubr
ggrepel package	Slowikowski[62]	https://doi.org/10.32614/CRAN.package.ggrepel
gridExtra package	Augie and Antonov[63]	https://doi.org/10.32614/CRAN.package.gridExtra
patchwork package	Pederson[64]	https://doi.org/10.32614/CRAN.package.patchwork
rgbif package	Chamberlain et al.[65]	https://doi.org/10.32614/CRAN.package.rgbif
scales package	Wickham et al.[66]	https://doi.org/10.32614/CRAN.package.scales
stringr package	Wickham[67]	https://doi.org/10.32614/CRAN.package.stringr
tidyverse package	Wickham et al.[68]	https://doi.org/10.32614/CRAN.package.tidyverse
zoo package	Zeileis and Grothendieck[69]	https://doi.org/10.32614/CRAN.package.zoo

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data sources for world insect dataset (Data S1)

The world numbers of described insect species per family (column "world_spp") as well as the major larval feeding group(s) per family (column "DETRI_world" through "BROOD_world") were obtained from various literature and databases, indicated in the column "reference". The corresponding Supplemental references are listed in the supplemental information.

Data sources for non-native insect dataset (Data S3)

The Linnean names of non-native species (column "genus_species") and their taxonomic order and family placement (columns "order" and "family"), as well as year of first record (column "year_first_record") in a given world region ("column "region") were obtained from Turner et al.[49] The world numbers of described insect species per family were taken from Data S1. The larval feeding group(s) for the individual species (where available) were obtained from various literature and databases, indicated in the column "reference". The corresponding Supplemental references are listed in the supplemental information.

METHOD DETAILS

We used the Turner et al. dataset[49] of non-native insect species for our global analyses, with comprehensive lists of non-native species for the following 11 regions: North America (Canada, continental USA), the Hawaiian Archipelago, Chile, Europe (including its major islands and the European part of Russia), South Africa, South Korea, Australia, and New Zealand, as well as Japan, the Nansei Islands and the Ogasawara Islands, the latter two of which were merged with Japan in order to harmonize the insect dataset with that of plant naturalisations[50] (see below). This resulted in records from nine world regions, with all continents except Antarctica represented (Figure S1). Data on insect invasions in the Galapagos Archipelago were not included in our analysis, as no list of naturalized plants was available for this region.[50] We excluded species reported as eradicated or intentionally introduced; the latter were

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excluded since their transport and establishment are driven by very different processes than species arriving accidentally. Furthermore, families with predominantly aquatic larvae were excluded, since aquatic insects are systematically under-represented among non-native assemblages worldwide.[70] Taxonomic cleaning was carried out based on the GBIF taxonomic backbone[51] using the R package 'rgbif'[65]; exceptions from the GBIF backbone taxonomy are listed in the legend of Data S1.

For each record of a non-native species in a given region, the year of first discovery was included in our analyses. Year of discovery was used as a proxy for the year of establishment which is in most cases unknown and predates the date of discovery.[42]

Numbers of native species were used as a baseline for quantifying over-representation of specific insect trophic groups among non-native species. Global numbers of described insect species per family were compiled from various sources, indicated in Data S1. To limit the stochastic effects of species-poor families, we restricted our analyses to families with at least 500 described species globally.

We researched the trophic group of each insect species in the non-native species dataset (Data S3) based upon the classification of the mode of feeding of immature stages (i.e. larvae) into five larval trophic groups: herbivory, predation, parasitism, detritivory, and brood-care. We standardized the classification on larval mode of feeding rather than adult feeding because feeding during immature stages tends to be more extensive than during the adult stage of most insect species, with some species not feeding at all as adults. While the trophic group classification system that we applied is widely used, there are other, more detailed classification systems available that 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 species, which serves as an obstacle for implementing more complex classification systems.

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 (incl. seeds) as well as sap-feeders and gall-makers that feed on plant tissue. *Predation* was defined as larval feeding on freshly killed animal tissue of more than one prey item and 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 is defined as larvae feeding on or inside a single living animal host organism.[7] This includes both parasitoids with invertebrate hosts and parasites of vertebrates. Although 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 the host's eggs or larvae, 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 group. *Detritivory* is circumscribed as larval feeding on detritus, dead and decaying animal and plant substrate (incl. tree bark), 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) consumes fungal hyphae growing on the decomposing matter. *Brood care* is applied to all 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. As stated above, kleptoparasites, although also engaging in brood care, were classified in the parasitism group.

For families in which all species fall in a single trophic group (e.g. all Aphididae are herbivores), it was possible to classify all species based on their family. But for species in "mixed" families (e.g. Staphylinidae contain herbivores, predators and detritivores) it was necessary to research each non-native species by searching the literature. Species occupying more than one trophic group were split into equal fractions of 1 (e.g. *Sinoxylon unidentatum*, a bostrichid beetle, was classified as 0.5 detritivory and 0.5 herbivory). We refer to this species-level dataset as the "non-native dataset" (Data S2).

We also estimated the proportion of world species in each family that fell into each of the five trophic groups (Data S1). Each of the families with 500 or more species globally was assigned a proportion of species falling in each of the five trophic groups ranging from 0 (no known species in the trophic group) to 1 (larvae of all known species in the trophic group). We refer to this as the "world-family dataset" (Data S1). For families with species falling into more than one trophic group, we estimated the fraction of species in each trophic group using increments of 10%, or smaller increments when specific species numbers were available. To accomplish this classification, we largely followed the feeding mode attributions in the "insect trait tool" dataset of German insects[52]; as that dataset is geographically confined to Germany, we adjusted proportions in numerous cases for our global approach. Species numbers per family trophic group were calculated by multiplying the relative proportion of each trophic group by the family's total species number and then rounding to the nearest integer. For example, for Dermestidae, proportions of 0.8 for detritivores and 0.2 for predators were each multiplied by 1200 global species resulting in 960 detritivorous species and 240 predator species.

QUANTIFICATION AND STATISTICAL ANALYSIS

Observed frequencies of trophic groups among non-native species were compared with trophic group frequencies for world species. Two-sample *z*-tests for equality of proportions with continuity correction were used to test for differences in group proportions between the two assemblages (Figure 1) using the prop.test function in the 'stats' R package.[53]

Temporal trends in establishments in each trophic group were compared with temporal trends in plant naturalizations. Time series of plant naturalizations were generated by filtering the Seebens dataset[50] for the same nine world regions (Data S4). 20-year moving window averages were calculated to illustrate invasion rates in plants and the five trophic groups. We detrended decadal sums of plant naturalizations and first records of herbivores as well as parasites by fitting simple linear regression models to the time series, and using residuals for cross-correlation analysis. The ccf function of the 'stats' R package[53] was used to calculate cross-

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correlograms between plants and herbivores (1700s to 2000s; Figure 2C) and between herbivores and parasites (1750s to 2000s; Figure 2D).

Temporal trends of trophic groups were quantified both as numbers of species in each trophic group over time and as proportion of the cumulative species in each trophic group over time. This was done for the dataset pooling the nine world regions together as well as individually for each of the five world regions with the most established non-native species (Australia, Europe, Hawaii, New Zealand, North America). Occurrences of non-native species in more than one of the nine world regions were considered independent invasion events and counted as such in the dataset of the pooled regions. The relatively few records prior to 1850 were excluded, as were those reported after 2009, since these showed signs of reporting lag.[71] To test for changes in trophic group proportions over time, we used the cumulative sums from the last year of each decade (1709, 1719 etc. for the world dataset, and 1859, 1869 etc. for the five regions) and employed Cochran-Armitage tests for trend over time (Figure 3H) using the R package 'DescTools'[58].

All analyses were run in R[53] using RStudio[54] and several R packages.[55–69] The R code is available in Data S5.