Moths and butterflies on alien shores – global biogeography of non-native Lepidoptera

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Abstract

Aim

Lepidoptera is a highly diverse, predominantly herbivorous insect order, with species transported to outside their native range largely facilitated by the global trade of plants and plant-based goods. Analogous to island disharmony, we examine invasion disharmony, where species filtering during invasions increases systematic compositional differences between native and non-native species assemblages, and test whether some families are more successful at establishing in non-native regions than others.

Location

Hawaii, North America, Galapagos, Europe, South Africa, South Korea, Japan, Nansei Islands, Ogasawara Islands, Australia, New Zealand.

Taxon

Lepidoptera.

Methods

We compared numbers of non-native, unintentionally introduced Lepidoptera species with the land area of 11 regions worldwide. Differences among native and non-native assemblages in the distribution of species among families were investigated using ordination analysis. We tested whether invasion disharmony is explained by propagule pressure (proxied by species richness in border interceptions) and if families were associated with specific trade commodities.

Results

In total, 741 non-native Lepidoptera species, accounting for 0.47% of the global diversity of lepidopterans, are established in at least one of the 11 regions. Crambidae, Pyralidae, Tineidae and Gracillariidae were particularly successful invaders, whereas the two most species-rich families, Erebidae and Geometridae, were under-represented among non-native Lepidoptera. Much of the variation in species numbers in the native, and less so in the non-native assemblages could be attributed to land area. Although native assemblages were similar among nearby regions, non-native assemblages were not, suggesting geography had little effect on invasion disharmony. Comparison of established with intercepted species revealed that macromoth families were generally under-represented in establishments, whereas several micromoth families were under-represented in interceptions. This discrepancy may relate to greater detectability of larger species or high propagule pressure via associations with specific invasion pathways.

Main conclusions

Invasion disharmony in Lepidoptera appears to be driven by processes unrelated to the success of native assemblages. While native assemblages developed through long-term evolutionary radiation, the composition of non-native assemblages is driven by differential invasion pathways and traits affecting the establishment of founder populations that vary among families.

Keywords

biological invasions, commodities, establishment, border interceptions, international trade, invasion disharmony, non-native region, propagule pressure

1. Introduction

Insects are by far the most diverse group of animals, and of eukaryotes in general. The over one million described insect species amount to 60% of all known animals (Zhang, 2013), and with an estimated 5.5 million total insect species, this percentage might be as high as 90% (Stork, 2018). Among insects, the order Lepidoptera (moths and butterflies) is one of the four largest groups. More than 157,000 species have been described (van Nieukerken et al., 2011), and an actual number of up to 500,000 species appears reasonable (Gaston, 1991). The majority of Lepidoptera larvae feed on various parts of plants, making this order one of the largest evolutionary radiations of herbivorous animals (Grimaldi & Engel, 2005). Lepidoptera also comprise numerous pest species of economic importance to agriculture and forestry. Notable pests include the polyphagous spongy moth, *Lymantria dispar*, on various deciduous and coniferous trees (Wu et al., 2020), *Ostrinia* corn borers and *Helicoverpa zea* on maize (Nafus & Schreiner, 1991; Olmstead, Nault & Shelton, 2016), the box tree moth, *Cydalima perspectalis*, on *Buxus* trees (Bras et al., 2019), *Chilo* and *Scirpophaga* stem borers as well as *Cnaphalocrocis*/*Marasmia* leaf-folders on rice (Bleszynski, 1970; Bradley, 1981; Lewvanich, 1981), and the tomato leaf miner *Tuta absoluta* on tomatoes (Desneux et al., 2010). The larvae of several groups of Lepidoptera, such as Tineidae, Oecophoridae, Cosmopterigidae, Pyralidae and Gelechiidae, feed on detritus and fungi, or on dry plant products such as grains, and can thus become serious pests of stored foods. With the global trade of plants and plant-based goods, Lepidoptera feeding on these products are inadvertently transported (Liebhold, Brockerhoff, Garrett, Parke & Britton, 2012), but some species may move via other, traditionally less well-inspected pathways such as in sea containers or with machinery (Toy & Newfield, 2010).

Lepidoptera appear to not establish equally well in different non-native regions, and this difference in species richness of non-native moths and butterflies may be linked to differences in land area among invaded ranges. Previous work on numerous plant and animal taxa in different world regions (e.g., Blackburn, Delean, Pyšek, Cassey & Field, 2016; Sax & Gaines 2006) has shown that numbers of non-natives follow a classic species–

area relationship, i.e., a log-log linear pattern between numbers of species and the area they inhabit (Lomolino, 2000). Furthermore, several studies have noted that within most animal and plant groups there are certain taxa that are systematically over- or under-represented in the flora and fauna found on oceanic islands compared to mainland source regions. This phenomenon, referred to as "island disharmony" (Carlquist, 1965), is thought to result from selective assembly mechanisms, such as filtering based on dispersal capacity, permitting only a subset of mainland species to successfully colonise islands (Gillespie & Roderick, 2002; König et al., 2020). Much like island disharmony, an analogous filtering of species may occur during biological invasions, producing systematic compositional differences between native and non-native assemblages. However, observation of such "invasion disharmony" has largely been limited to family-level composition between native and non-native plant assemblages (Procheş, Wilson, Richardson & Rejmánek, 2008; Pyšek, 1998; but see e.g., Blackburn & Duncan, 2001; Dugdale, 1988), though Liebhold et al. (2021) recently reported such a pattern for beetle (Coleoptera) family-level composition.

Observed patterns of invasion disharmony are likely the result of taxon-specific traits that influence either propagule pressure (rate of species transport to the non-native region) or invasiveness (probability of establishment following introduction) (Liebhold et al., 2021). Unfortunately, differentiating between these two mechanisms can be challenging since it is typically impossible to directly measure either. However, measurements of species richness in interceptions during port inspections may serve as a proxy for propagule pressure. Even though species richness in interceptions may be influenced by a variety of factors other than propagule pressure, it is still strongly related to arrival rates and statistically related to historical establishments (Brockerhoff, Kimberley, Liebhold, Haack & Cavey, 2014; Turner et al., 2020). Furthermore, comparing interceptions with establishments may indirectly allow for comparison of the invasiveness among groups of species (Colautti, Grigorovich & MacIsaac, 2006).

Knowledge of which Lepidoptera families have a higher probability of establishment would be useful in predicting invasion risk for specific, potentially damaging species. This predictive knowledge and information about associations of various Lepidoptera groups with different import commodities could be used to prioritise biosecurity efforts. The objectives of this study thus are to 1) identify Lepidoptera families that are the most successful at establishing in non-native regions, 2) investigate to what degree land area accounts for the diversity of established non-native species among regions, 3) investigate disharmonies between established and native species for 11 world regions, 4) determine if observed invasion disharmony can be explained by differential propagule pressure (as proxied by intercepted species richness during port inspections), and 5) investigate associations of various Lepidoptera groups with specific classes of trade commodities transported in international trade and travel.

2. Material & Methods
2.1 Compilation of species lists
We assembled lists of native and non-native established Lepidoptera species from 11 different regions worldwide for which comprehensive data on native and introduced Lepidoptera species exist. These 11 regions are: North America (Canada, continental USA), the Hawaiian Archipelago, the Galapagos Archipelago, Europe (including its major islands and the European part of Russia), South Africa, South Korea, Japan (excluding the following two regions), the Nansei Islands, the Ogasawara Islands, Australia, and New Zealand (Appendix S1). We acknowledge that these regions mostly coincide with countries with highly developed economies. It was only from these regions that we could practically obtain comprehensive lists of established non-native species. The comprehensive species lists (see references in Appendix S1) had largely already been

published, and we made efforts to update them and correct errors. A list of names of these non-native species per region is given in Appendix S5. These data form part of a larger database, "International Non-native Insect Establishment Data", that is periodically updated and freely available (Turner, Blake & Liebhold, 2021). We recognise that these lists of non-native species may be incomplete, as there typically are lags between establishment, discovery and reporting of new non-native species (Essl et al., 2011; Morimoto, Kiritani, Yamamura & Yamanaka, 2019).

Taxonomic delimitation of Lepidoptera families and total species numbers per family follows van Nieukerken et al. (2011), Zahiri et al. (2011, 2012, 2013), Kaila, Epstein, Heikkilä & Mutanen (2013), Kaila, Nupponen, Gorbunov, Mutanen & Heikkilä (2020), Sohn et al. (2013), Heikkilä, Mutanen, Kekkonen & Kaila (2014), Regier et al. (2014, 2015) and Kristensen et al. (2015). We kept the polyphyletic Batrachedridae (Heikkilä et al., 2014) in the circumscription of van Nieukerken et al. (2011). *Chrysodeixis chalcites* and *Ch. eriosoma* (Noctuidae) are indistinguishable in morphology and DNA Barcode sequence and were thus treated as one species, as their status as separate species is currently not resolved. Species lists from each region were standardised to overcome duplication through synonyms and misspellings, by performing taxonomic "cleaning" so that all species names and higher-level taxon designations were based on a single taxonomic classification system (Supplement S1: Figure S4). This was performed using the GBIF taxonomic database (GBIF Secretariat, 2019) and the 'taxize' version 2 package in R (Chamberlain & Szöcs, 2013). Code used for this taxonomic cleaning is available in the Zenodo repository (Blake & Turner, 2021). Though most user-supplied Lepidoptera species names were recognised (including as synonyms or misspellings) in the GBIF backbone taxonomy, a small number were not, and standardisation was performed manually via searches of alternative databases (Beccaloni et al., 2003; Nuss et al., 2003–2022; De Prins & De Prins, 2006–2022, 2011–2022; Gilligan, Baixeras & Brown, 2018) and manual online researching of names.

Comparison of native and non-native established species assemblages was done at the family level by summarising the number of non-native and total species for each Lepidoptera family present in each region. Species known to have been intentionally introduced (e.g., biological control agents) were excluded from our analyses, as we were interested in patterns that result from accidental invasion processes (but see Appendix S10 for the results of non-native established species *including* intentionally introduced species). The numbers of intentionally introduced species per family and region are given in Appendix S4; they are also included in Appendix S5 and marked in the column "intentional_release" with "yes". Numbers of native species per family and region were calculated by subtracting from the total number of species (Appendix S2) the number of non-native established species (Appendix S3) as well as the intentionally introduced non-native species (Appendix S4). To limit the stochastic effects of species-poor families, we restricted our analyses to families with at least 10 non-native species present among the 11 regions. Exceptions were the analyses on the proportional representation of families in establishments and interceptions (see 2.3 and 2.5), where all families containing established non-native species were included, as the underlying binomial model takes into account the stochastic behaviour expected by smaller families. To illustrate differences in numbers of native or non-native species among the 11 regions, a cluster heatmap was generated.

2.2 Species–area relationships

To analyse the influence of the different land area of regions on species richness, we plotted log numbers of species per regional assemblage against log regional land area (species–area relationships), with slope and R^2 calculated for the linear regression relating log species numbers to log land area. This log-log linear relationship is a standard approach used for explaining geographical variation in biological diversity

(Lomolino, 2000). Species–area plots were generated for the total number of native and non-native Lepidoptera species from each region. The same was done for the two families with the most non-native species among the 11 regions.

2.3 Scatterplots for proportional representation of families

For each of the 11 regions, we compared observed and expected numbers of non-native with numbers of native species per family in that region. The expected number of species per family was calculated assuming an equivalent proportion of species in each family in the native species assemblage. To illustrate variation in invasion disharmony among regions, we generated scatterplots of numbers of non-native species per family against numbers of species in the same family for the native assemblage for each of the 11 regions. The scatterplots include a line of equivalent proportions as well as bounds about this line, which were calculated as the quantiles of the binomial distribution. Any families which fell outside these bounds were deemed over- or under-represented at the α=0.01 level, using a Bonferroni correction (Dunn, 1961) to account for multiple comparisons among families. A similar scatterplot was generated comparing non-native species richness of each family pooled among the 11 regions versus the number of world-described species per family.

2.4 Ordination analysis

 A direct ordination, redundancy analysis (RDA) was performed to characterise differences among all native and non-native assemblages based upon the distribution of species among families in each assemblage (ter Braak, 1986; Legendre & Legendre, 1998). The scores of each assemblage were plotted for the first two RDA axes, with the position of each assemblage in this space providing a map of compositional similarities or dissimilarities among assemblages. To visualise the relationship of the differences among assemblages to the relative dominance of different families, we also plotted RDA scores of each family. A permutation test based on 999 permutations evaluated the effect of native or non-native status and of regions, including both the pooled set of all non-native species and the world described species. Neither crossed nor nested effects were considered. The RDA and permutation tests were computed using the 'vegan' package in R (Oksanen et al., 2019). To account for the skewed distributions of numbers of species per family in the correlation and ordination analyses, species richness of each family in each of the assemblages was transformed using a Hellinger transformation (Legendre & Gallagher, 2001) as the square root of the number of native or non-native species per family divided by the total number of native or non-native species per region.

2.5 Interception data

As a proxy for propagule pressure for each Lepidoptera family, we quantified species richness for each family among Lepidoptera species intercepted at sea- and airports. These data were sourced from regions that largely overlapped with the regions investigated for the establishments: North America (mainland USA, Canada), Hawaii, the western countries of the European and Mediterranean Plant Protection Organization (EPPO), UK, South Africa, Japan, South Korea, Australia and New Zealand. The data spanned different time frames from the 1990s to the 2010s; see Appendix S1 for more details. We are aware that the differences in interception recording between EPPO and the other countries may have introduced a bias. However, the EPPO interceptions represented only 2% of the entire interception dataset, so the effect of this bias on our results would be limited. We also acknowledge that inspections are generally not conducted randomly; focused inspection of certain commodities may introduce bias in summaries of pathway associations. Furthermore, inspections do not quantify the degree of infestation. Thus, interceptions only detect a small fraction of arrivals, and their primary value is for monitoring pathways and compliance checking; in most cases, inspection contributes little to directly preventing arrival of insects. Data from the different regions

were pooled to quantify species richness for Lepidoptera families. These border interception data are described in detail in Brockerhoff et al. (2014), Turner, Brockerhoff et al. (2021) and Saccaggi et al. (2021).

To investigate whether propagule pressure (proxied by border interceptions) can explain invasion disharmonies observed in the non-native assemblages, a scatterplot of numbers of intercepted species per family against numbers of species in the same family for the world assemblage was generated, analogous to that for established species. Furthermore, a scatterplot comparing established non-native species richness per family (pooled from the 11 regions) with numbers of intercepted species per family was generated to determine the extent to which variation in interception frequency among families explains variation in establishment frequency.

2.6 Commodity data
Data on trade commodities associated with Lepidoptera intercepted during inspections and identified at least to genus level were derived from the interception data described above. However, the commodity dataset represented a geographical and temporal subset because commodities were not recorded for all interceptions; in addition, the commodity data from New Zealand came from an earlier period (1960–2000) (compare Figures S2 and S3, and Tables S2 and S3 in Appendix S1). Data were pooled from interceptions at sea- and airports of six regions (USA incl. Hawaii; Canada; EPPO; Japan; Australia; New Zealand), and span different timeframes from 1950 to the late 2010s (Appendix S1). Data from each region were pooled to quantify species richness for each Lepidoptera family. The data span 14 classes of commodities (see Appendix S8), based on the Harmonized Commodity Description and Coding System developed by the World Customs Organization (https://www.trade.gov/harmonized-system-hs-codes). To limit the impact of stochastic effects, analyses were restricted to families with more than 100 commodity records (Appendix S8). Plant product commodities of these families were itemised to 10 subclasses for a more fine-scaled analysis of pathways (Appendix S9). Data collection and processing of commodities data is described in detail in Fenn-Moltu et al. (in review).

3. Results
3.1 Species richness per region
Of the 1,178 total records of established non-native Lepidoptera species in the 11 regions, 113 records were for 98 intentionally introduced species. After exclusion of the records for these species, the dataset for analysis contained 1,065 non-native species records, representing 741 species in 59 families. North America had the most recorded non-native species, followed by Hawaii and New Zealand (Table 1). The fewest non-native species were found in the Ogasawara Islands, South Korea, Japan and the Nansei Islands. The highest percentage of non-native species among total species was observed for the Galapagos Islands, with 19.4 %, followed by the Hawaiian Islands (16.6 %), and the lowest for South Africa (0.4%) and South Korea (0.8%) (Table 1).

Sixteen of the 59 Lepidoptera families with non-native species contained 10 or more non-native species in at least one of the 11 investigated regions (Table 2), referred to as 'top-16 families' hereafter. The six most widespread non-native species in the dataset, which are present in at least eight of the investigated regions, comprise two Pyralidae (*Cadra cautella*, *Plodia interpunctella*), two Gelechiidae (*Phthorimaea operculella*, *Sitotroga cerealella*), one Pieridae (*Pieris rapae*), and one Plutellidae species (*Plutella xylostella*).

Table 1. Numbers of total and non-native Lepidoptera species among investigated regions. Numbers in brackets indicate the additional number of intentionally introduced species, which were excluded from the number of non-native established species in the analyses.

Region	Number of total spp.	Number of non-native spp.	Percent non-native spp. among total spp. of region
North America (excl. Mexico)	12,803	300 (14)	2.3
Hawaiian Islands	1,136	189 (32)	16.6
Galapagos Islands	360	70 (0)	19.4
Europe (incl. islands and European part of Russia)	10,669	95 (3)	0.9
South Africa	7,935	28 (9)	0.4
South Korea	2,793	22 (0)	0.8
Japan (excl. Nansei and Ogasawara Islands)	4,590	46 (2)	1.0
Nansei Islands	1,417	48 (0)	3.4
Ogasawara Islands	276	11 (0)	4.0
Australia	12,476	106 (43)	0.8
New Zealand	1,694	150 (10)	8.9
All regions		741 (98)	
World	158,293		

Table 2. Summary of the 16 Lepidoptera families with 10 or more non-native species established in at least one of the 11 investigated regions. Numbers in brackets indicate the additional numbers of intentionally introduced species.

Lepidoptera family	Number of non-native spp.	Number of world spp.	Percent of non-native spp. among world spp.
Noctuidae	83 (6)	11,772	0.7
Crambidae	83 (12)	10,441	0.8
Tortricidae	70 (12)	10,387	0.7
Erebidae	63 (7)	24,569	0.3
Pyralidae	57 (10)	6,200	0.9
Tineidae	47 (0)	2,393	2.0
Gelechiidae	37 (5)	4,700	0.8
Geometridae	27 (3)	23,002	0.1
Gracillariidae	26 (5)	1,866	1.4
Oecophoridae	25 (0)	3,400	0.7
Nymphalidae	15 (2)	6,152	0.2
Pterophoridae	13 (5)	1,318	1.0
Depressariidae	12 (3)	2,300	0.5
Cosmopterigidae	11 (0)	1,730	0.6
Coleophoridae	11 (2)	1,400	0.8
Lycaenidae	11 (2)	5,201	0.2

In the heatmap of native families (left panel in Figure 1), the relatively species-rich Hawaiian Cosmopterigidae stand out among the generally species-poor families, as do the Oecophoridae in Australia, where two thirds of the global species in this family are found. Among the non-native assemblages (right panel in Figure 1), Pyralidae and Tineidae are generally the most species-rich families across most of the regions. Non-native Crambidae were especially species-rich on the Galapagos archipelago, where non-native species comprise one third of all Crambidae.
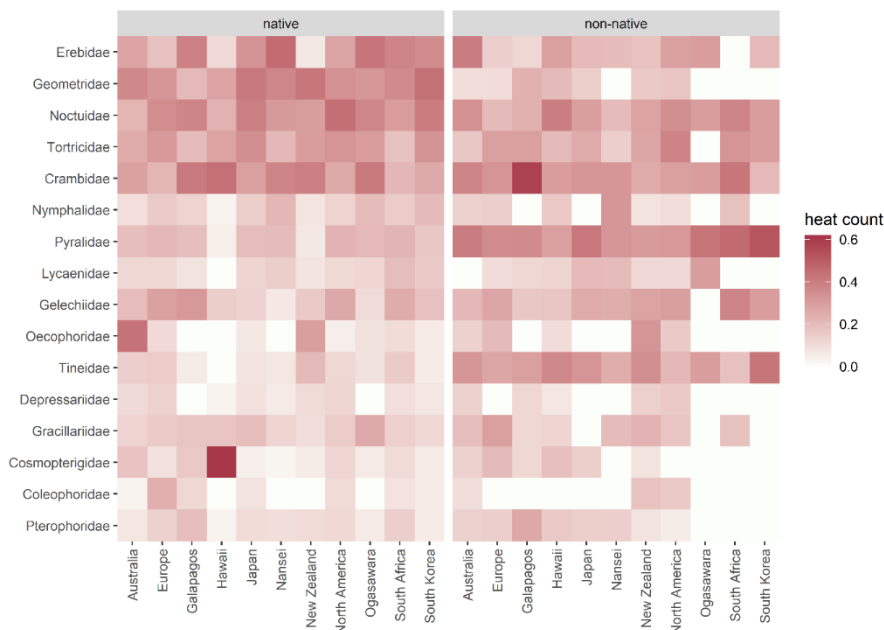
Figure 1. Heatmap of number of species within each family for native (left panel) and non-native (right panel) Lepidoptera for each region. Values are calculated as √(number of native or non-native species in a family per region / total number of Lepidoptera per region).

3.2 Species–area relationships

We observed a classic log–log linear species–area relationship for the total numbers of native (Figure 2a; R^2 = 0.8264, p < 0.005) and non-native (Figure 2b; R^2 = 0.3338, p = 0.06269) species per region. This shows that much of the variation in native species richness, but not in non-native richness, is attributable to the land area of each region. A similar pattern was observed for the two most species-rich families of non-native Lepidoptera, Noctuidae and Crambidae (Figure 2c–f). Land area generally explains more than twice as much of the variation in numbers of native species as variation in numbers of non-natives (Appendix S6). Species-area relationships for the 14 less species-rich families of the top-16 families showed the same general pattern (Appendix S6: Figure S6) except for non-native Geometridae, Nymphalidae, Pterophoridae and Coleophoridae. As the numbers of non-native species per family declined, small sample sizes created proportionally greater stochastic influences and erratic species-area relationships in several families.
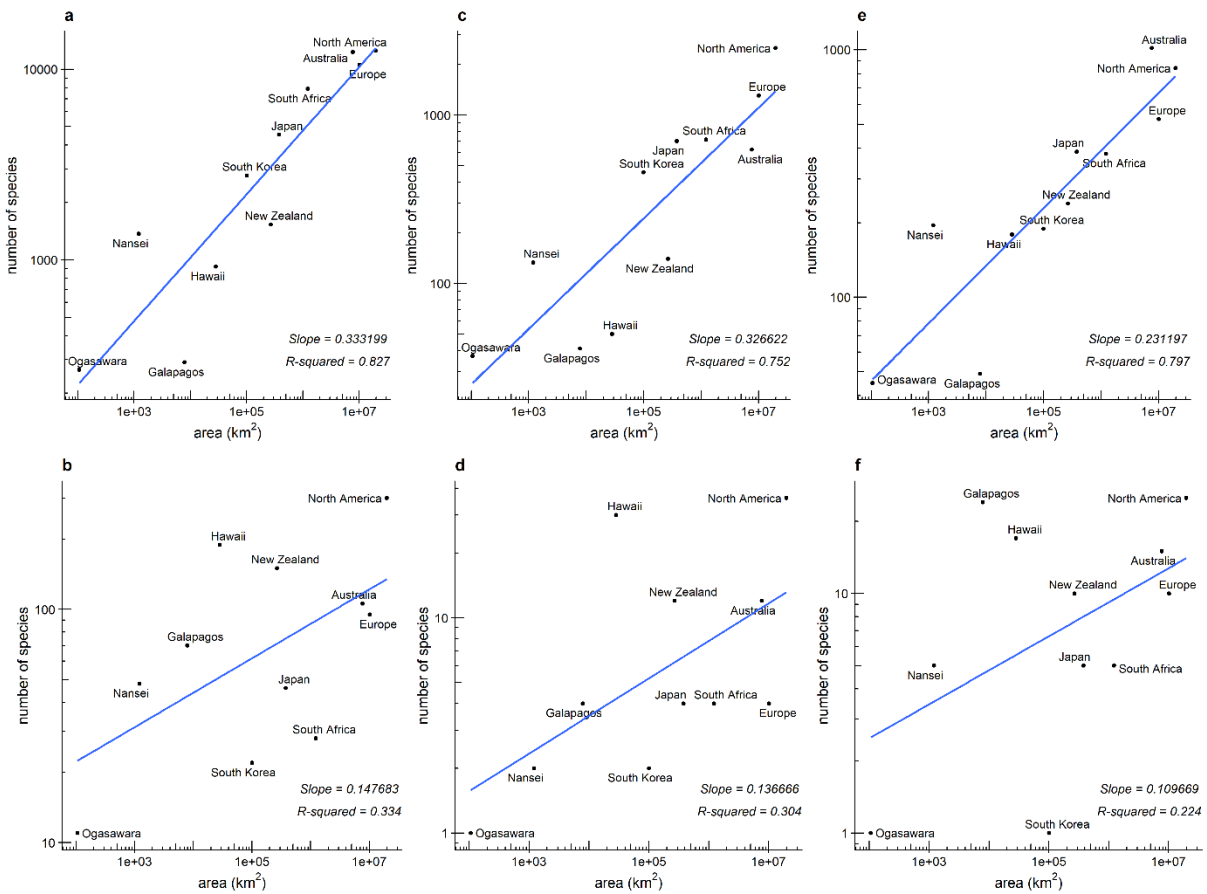
Figure 2. Log-log species–area relationships in the 11 investigated regions for a) all native Lepidoptera species, b) all non-native Lepidoptera species, c), native Noctuidae, d) non-native Noctuidae, e) native Crambidae, f) non-native Crambidae.

3.3 Proportional representation in establishments

Pyralidae were over-represented in relation to what was expected according to native species in the non-native assemblages of five of the 11 regions, and Tineidae were over-represented in seven (Figure 3). Geometridae were under-represented in the non-native assemblages of four regions.
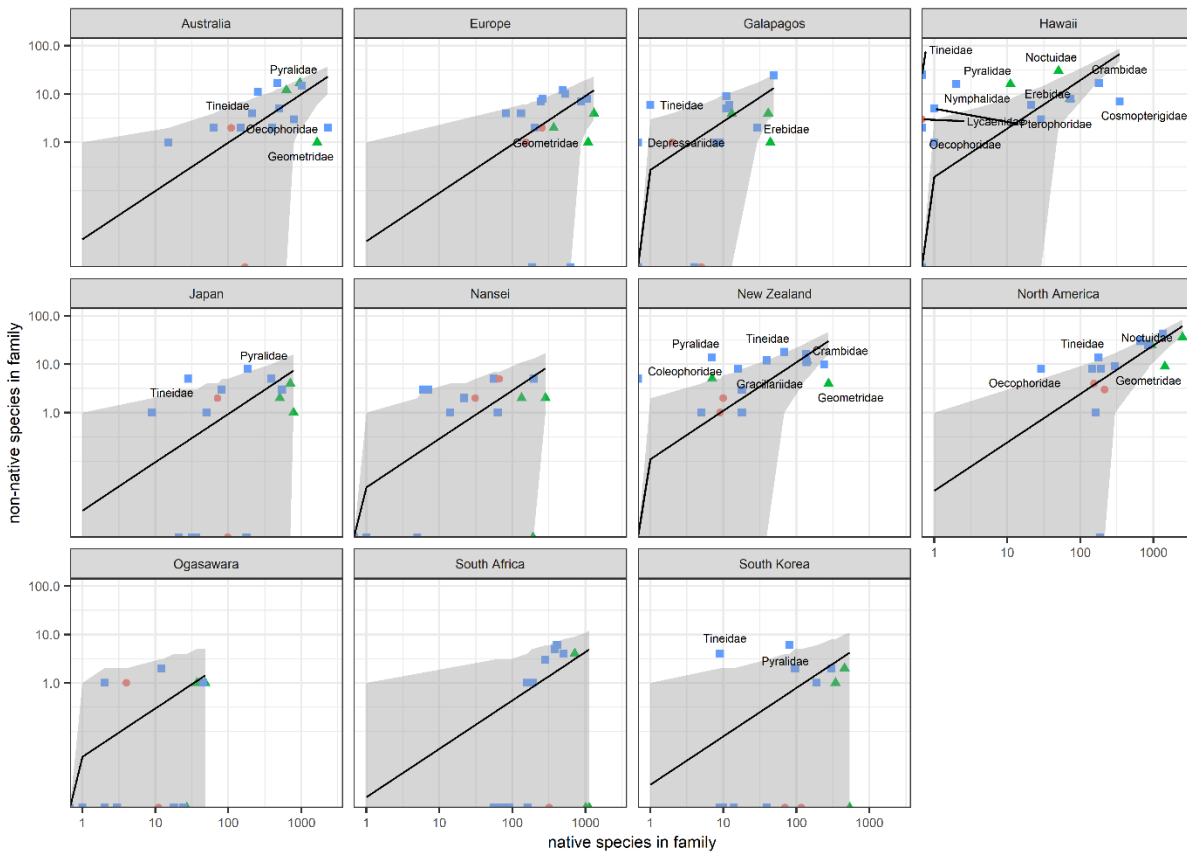
Figure 3. Scatterplots of the numbers of non-native species per family (y-axis) versus numbers of native species per family (x-axis) for the 11 different regions. Red circles: butterflies, green triangles: macromoths, blue squares: micromoths. For Hawaii, Nymphalidae fall on the same point and obscure the Pterophoridae. Black line describes expected non-native species numbers per family if in same proportions as in the globally described species; grey shading indicates the α=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- or under-represented.

In the scatterplot of the pooled data from all 11 regions (Figure 4a), six of the 59 families containing non-native species were outside the proportions expected from their frequencies in the world fauna: Geometridae and Erebidae were under-represented, whereas Crambidae, Gracillariidae, Pyralidae and Tineidae were over-represented in the non-native assemblage.
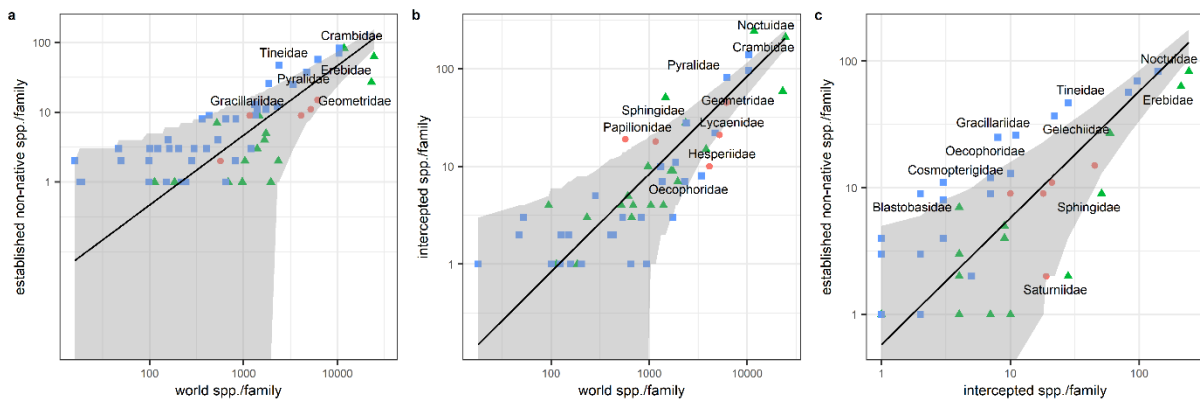
Figure 4. Scatterplots of a) total numbers of established non-native species per family pooled among all 11 regions (y-axis) versus global numbers of species per family (x-axis), for all 59 families comprising non-native species; b) intercepted species per family versus global numbers of species per family; and c) established non-native species per family versus intercepted species per family. Red circles: butterflies, green triangles: macromoths, blue squares: micromoths; black line describes expected non-native species numbers per family if in same proportions as in the globally described species; grey shading indicates the α=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- or under-represented.

3.4 Ordination analysis

Ordination analysis (RDA; Figure 5) showed that the family-level composition of non-native assemblages is strongly distinct from that of native assemblages (F = 8.2185, p = 0.001). This difference is evident in the general positioning of non-native (red in Figure 5a) and native (blue in Figure 5a) assemblages on opposite sides of the ordination space, primarily defined by the first (RDA1) axis. Region, however, had no significant effect (F = 1.1186, p = 0.308), since family-level composition of non-native and native assemblages from the same region were not more similar to each other than to other assemblages. Although native assemblages were of a similar composition in geographically nearby regions (especially Australia and New Zealand), the non-native assemblages were generally not (Figure 5a). Loadings for the first RDA axis (Figure 5b), which separates native and non-native assemblages (Figure 5a), indicated that native assemblages were associated with relatively large numbers of Geometridae. Non-native assemblages, on the other hand, were associated with relatively high numbers of Pyralidae and Tineidae. The second axis (RDA2 in Figure 5b) was positively related to the fraction of Erebidae, and negatively associated with the fraction of Oecophoridae. The loadings for those two families were isolated, indicating that the relative species richness of Erebidae and Oecophoridae does not co-vary closely with those of other families.
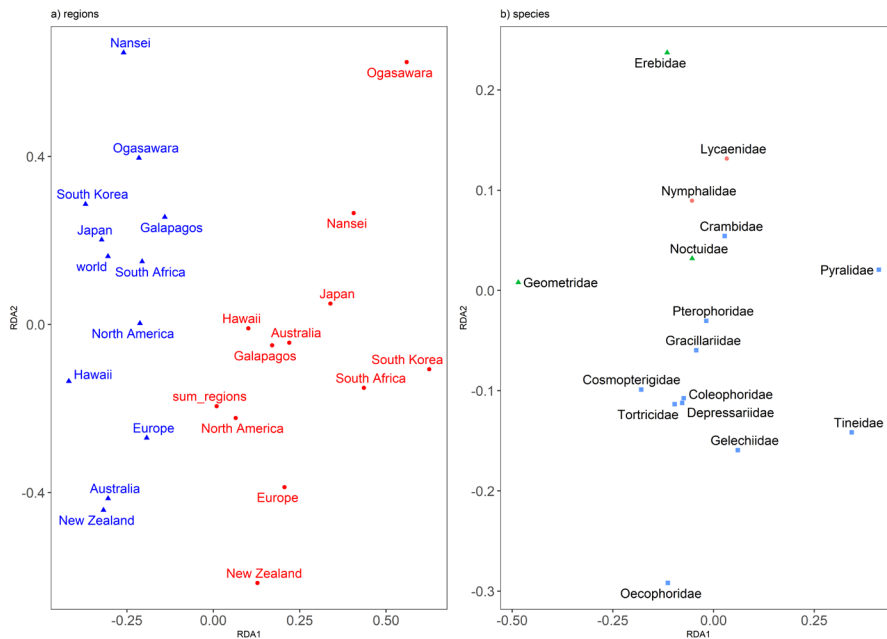
Figure 5. Results of RDA ordination on numbers of species per family. a) location of each region in space defined by the first two RDA axes; blue triangles are native assemblages, red dots are non-native assemblages; "sum_regions" refers to the sum of unique non-native species pooled from the 11 regions. b) loadings for the 16 Lepidoptera families with at least 10 established species; red circles: butterflies, green triangles: macromoths, blue squares: micromoths.

3.5 Proportional representations in interceptions

The interception dataset comprised 113,185 records from 52 Lepidoptera families (Appendix S7). Five occurred at frequencies greater than expected based on their frequencies in the world fauna (Figure 4b): Crambidae, Noctuidae, Papilionidae, Pyralidae and Sphingidae. In contrast, Geometridae, Hesperiidae, Lycaenidae and Oecophoridae were under-represented, i.e., they were considerably less frequently intercepted than expected from their global species richness. The comparison of established non-natives with intercepted species (Figure 4c) showed that the macromoth families Erebidae, Noctuidae, Saturniidae and Sphingidae were under-represented, whereas six micromoth families (Blastobasidae, Cosmopterigidae, Gelechiidae, Gracillariidae, Oecophoridae, Tineidae) were under-represented in the *interceptions* (and thus over-represented in the non-natives), i.e., there were substantially more established non-native species in these families than their interceptions would suggest.

3.6 Commodities

Interceptions of 43 families were recorded in association with specific commodities (Appendix S8), and 19 of these families had 100 or more interceptions. The majority of interceptions in these 19 families was from plant products (average 82.5%), followed by wood products (6.32%), machinery and electrical commodities (4.65%), stone and glass commodities (1.9%) and animal products (1.35%). The families with the highest proportion of interceptions on wood products were Geometridae, Cossidae and Nolidae (Figure 6a). Sphingidae stand out with a small proportion (27.3%) of reports from plant products, but a large proportion (46%) from machinery and electrical commodities – potentially an artefact of the small number of 198 records. Within the commodity class of plant products (Appendix S9), three commodities dominate: live plants/cut flowers, vegetables, and fruit/nuts (Figure 6b).
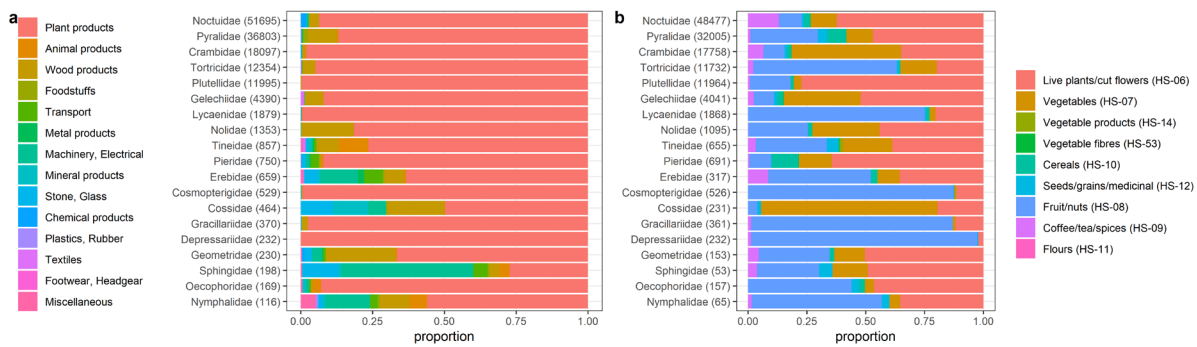
Figure 6. Trade commodities from which Lepidoptera were intercepted. a) Commodity classes and their proportions of the most commonly intercepted Lepidoptera families (n ≥ 100 interceptions). b) Commodities within the Plant products commodity class for the families in a). Numbers in brackets behind families indicate numbers of interceptions.

4. Discussion

We found 59 families of Lepidoptera (out of 138 families in total) with at least one non-native species established among the 11 investigated regions. The four families with the greatest numbers of established non-native species (Noctuidae, Crambidae, Tortricidae and Erebidae) are also among the five globally most species-rich families. Altogether, these 59 families comprise 741 non-native Lepidoptera species. This number is considerably smaller than the 1,967 non-native beetle (Coleoptera) species reported in a similar study that focused on the same regions except for South Africa (Liebhold et al., 2021). However, in these 10 regions, non-native Lepidoptera species represent 0.47% of the 158,293 global species – remarkably similar to the 0.51% of species of beetles that have established in at least one of the 10 regions investigated in Liebhold et al. (2021). Generally, however, Lepidoptera tend to be less well represented among alien assemblages as compared to other insect orders (Liebhold et al., 2016).

The observation that numbers of species increase with the area they inhabit – the species–area relationship – is perhaps the most general pattern in biogeography (Lomolino, 2000). Our results show that non-native Lepidoptera assemblages tend to follow this log–log linear species–area relationship, although land area explains less of the variation in non-native species numbers than it does for native assemblages (Figures 2, S6). Furthermore, the slopes of species–area relationships for non-native assemblages were generally half that of the native assemblages, often due to a high ratio of non-native to native species for small island regions versus a generally low ratio for large areas like North America, Australia and Europe (Table 1). A strong connection between land area and species richness may not entirely be a direct causal relationship: Liebhold et al. (2018) found that land area directly influenced native and non-native plant diversity, which in turn influenced the species richness of native and non-native insects.

In three island regions (Galapagos, Hawaii, and New Zealand), non-native species make up 9–20% of the region's total Lepidoptera fauna (Table 1). All three regions have experienced a strong influx of non-native flora and fauna in the past, shifting the composition of the local biodiversity. These patterns reflect the general tendency of oceanic islands to be more frequently invaded, as seen in various plant and animal groups (Blackburn et al., 2016; Moser et al., 2018). In these groups, invading species also tend to have greater impacts on native communities on islands compared to mainland environments, but it remains to be determined if this is a generalisable trend for Lepidoptera invasions.

The general concordance in the richness of families in non-native assemblages compared to native assemblages in a region (Figures 3, 4a) may reflect the availability of niches and the lack of competitive exclusion. But the concordance of richness of families in non-native assemblages with that of the world fauna may also reflect the availability of species in source species pools. Differentiating these two influences is likely difficult.

In addition to differences in the numbers of non-native Lepidoptera species among regions, we found differences in the composition of native and non-native assemblages reflecting invasion disharmony. The two families most over-represented in non-native assemblages were the Pyralidae, comprising many pests of stored food products, and the detritivorous Tineidae. Furthermore, we found non-native Lepidoptera to be dominated by micromoth families; only five of the top-16 families were macromoths and butterflies. Generally, micromoth families were over-represented in the non-native assemblages of establishments among the 11 investigated regions (Figure 3), and the same was true for the total numbers of established non-native species per family pooled among all 11 regions (Figure 4a). Hawaii is an exception, featuring two families of macromoths (Noctuidae, Erebidae) and one family of butterflies (Nymphalidae) among the over-represented families. At least the over-representation of non-native Nymphalidae in Hawaii can be explained by a low number of native nymphalids (Figure 1). Similarly, the under-representation of non-native Crambidae in Hawaii and New Zealand, of Cosmopterigidae in Hawaii, of Erebidae in Galapagos, and of Oecophoridae in Australia, can be explained by the proportionally large native species radiations in these regions, especially in the case of Hawaiian cosmopterigids (Figure 1). For the macromoth family Geometridae, no such pattern is apparent, suggesting that this family is indeed under-represented in the non-native assemblages of four of the 11 regions. Our findings of greater establishment success of micromoth families is consistent with those of Lawton & Brown (1986) for the establishment success of different insect orders in Great Britain: the smaller the body size, the higher the probability of establishment.

Four micromoth families (Crambidae, Gracillariidae, Pyralidae, Tineidae) stand out as more successful in non-native fauna than expected based on their global species richness. Their establishment success is likely attributable to their generally small body size, and to their larval life strategies: polyphagy in certain groups of Crambidae, fungi- and detritivory (including feeding on stored food products) in Pyralidae and Tineidae, and concealed (often internal) feeding in Gracillariidae and Tineidae. These traits either promote their association with imported goods, impede detection during border inspections, facilitate reproduction and subsequent establishment of invading populations, or act in combination.

Surprisingly, the two most species-rich families of Lepidoptera, Erebidae and Geometridae, are generally less successful invaders. Only 0.3% and 0.1% of their world species are among the non-native species present in the 11 investigated regions (Table 2). Many Geometridae species are host specialists, potentially limiting their ability to locate host plants in non-native areas and to successfully establish. Furthermore, Geometridae comprise by far the largest number of species among Lepidoptera (apart from Psychidae) with some sort of wing reduction (Sattler, 1991). The adults are generally weak flyers, and in numerous species the females are flightless, making this family one of the most philopatric groups among larger moths. After arrival in a non-native region, this might impede local spread but promote establishment of viable populations (Robinet & Liebhold 2009; Shaw & Kokko, 2015). In the Erebidae, the majority of species established in the 11 regions feed on more than one host plant family, and several species are extremely polyphagous: *Achaea janata* (subfamily Erebinae) feeds on 31 families of plants, *Lymantria dispar* (Lymantriinae) on 38 families, and *Hyphantria cunea* (Arctiinae) on 43 families (Robinson, Ackery, Kitching, Beccaloni & Hernández, 2010).

Analysing Erebidae at the subfamily level, especially for the species-rich Arctiinae and Lymantriinae, might provide a more detailed picture of establishment success within these subfamilies, but the small numbers of non-native species within each subfamily precludes a meaningful analysis here.

We used the most up-to-date and comprehensive phylogenetic classification system available; nonetheless, phylogenetic research in large groups such as Geometridae, Gelechiidae, Noctuidae and Erebidae is ongoing, with the circumscriptions of many families in flux. For example, considering in our analyses Pyralidae in the pre-Minet (1982) sense (i.e., including Crambidae), or Noctuidae as circumscribed before the recent changes in Noctuoidea systematics (Zahiri et al., 2010, 2011, 2012, 2013), would have led to considerably different results, where Pyralidae *sensu lato* (including Crambidae) with altogether 140 species would constitute the largest family of non-native Lepidoptera; and Erebidae, without the inclusion of the former Lymantriidae and Arctiidae, would comprise a lower number of non-native species. The classification of Lepidoptera used here thus reflects only a temporary state that may change as phylogenetic relationships are researched in more detail. Future studies on lower systematic levels (subfamilies, tribes) may uncover a more detailed picture of establishment success among non-native Lepidoptera.

The RDA redundancy analysis yielded no significant effect of region, indicating that native and non-native assemblages from the same regions are not significantly more similar to each other than to other assemblages. Furthermore, non-native and native assemblages were completely distinct from each other at the family level in the RDA ordination space (Figure 5a), indicating that the composition of non-native assemblages is driven by different factors compared to the drivers of native species richness. Similar results were observed by Liebhold et al. (2016) for insect assemblages at the order level, and by Liebhold et al. (2021) for beetle assemblages at the family level: in both cases, the composition of native assemblages was distinct from non-native assemblages. The processes determining the composition of native assemblages, which formed through long-term evolutionary radiation, and non-native assemblages are very different and likely explain their distinctness. Much like island disharmony, invasion disharmony can be considered to result from a filtering process that occurs when species are "moved" from the pool of native species in various world regions, arrive and successfully establish. During this process, some species are more likely to become associated with commodities that are transported internationally; life history traits of insects (e.g., their presence in grain or other material that is traded in high volumes) as well as their general abundance may influence the probability that they arrive in areas outside of their native range (Meurisse, 2019; Gippet et al. 2019). Other traits, such as their use of widespread host plants, may affect the likelihood of establishment following arrival. Together, these traits can form "invasion syndromes" (Novoa et al., 2020), which filter the pool of potential invaders resulting in some groups of species to be either over- or under-represented in non-native assemblages – factors that depend on the species' life history traits and that vary among insect orders and families (Kiritani & Yamamura, 2003; Liebhold et al., 2016; Meurisse et al., 2019).

The over-representation of Noctuidae, Crambidae, Pyralidae, Sphingidae and Papilionidae among intercepted groups (Figure 4b) may reflect, at least in part, high arrival rates (propagule pressure) linked to behaviours that cause them to become associated with specific transport pathways. Crambidae and Pyralidae are over-represented among both non-natives (Figure 4a) and intercepted species (Figure 4b). High propagule pressure (as high numbers of interceptions) may thus explain, at least in part, their establishment success. However, differences in the detectability of immature life stages may introduce biases in interception frequencies; large eggs and larvae in groups such as swallowtail butterflies (Papilionidae) and hawkmoths (Sphingidae) are easier to notice than those of Microlepidoptera with smaller eggs and more

cryptic caterpillars. A family-level comparison of established with intercepted non-native species (Figure 4c) supports this: six micromoth families are more successful at establishing than their interception numbers would suggest, indicating that they might be overlooked more often in interceptions. Among these, the larvae of Cosmopterigidae, Gelechiidae and Gracillariidae are mainly leaf- or fruit-miners, and those of Blastobasidae, Oecophoridae and Tineidae are generally fungivores and detritivores. Their concealed feeding likely impedes their detection during inspections, and especially when present in their egg stage, many of the species in these families may be overlooked during inspections. Body size thus appears to affect the detectability of Lepidoptera in interceptions. This could explain why Tineidae, the most frequently over-represented family in the establishments among the 11 investigated regions, was not over-represented in interceptions. However, we currently cannot distinguish whether this observation is due to their below-average frequency of detection in inspections, or whether high propagule pressure may not be a strong factor driving the establishment success of Tineidae, and potentially other Lepidoptera groups.

Since we did not attempt to characterize patterns of establishment through time, time lags between establishment and discovery are unlikely to impact our analyses. However, many of the species currently established may have arrived many years prior to the period from which our interception data were recorded, and this may introduce some artifactual differences when comparing patterns. On the other hand, Nahrung & Carnegie (2021) found that non-native forest insect species that established in Australia in early years were generally still intercepted in high numbers long after their establishment, indicating that contemporaneous interceptions are still are good indicator for previous establishments.

The larvae of the vast majority of butterflies and moths are herbivorous, and Lepidoptera are thought to have radiated in tight connection with the diversification of angiosperms (Kawahara et al., 2019). It is therefore not surprising that we find the majority of Lepidoptera to be intercepted from plant products, although this observation might be somewhat biased, as plant products, and among them especially live plants, fruits and vegetables, tend to be one of the most intensively inspected commodities (Eschen, Roques & Santini, 2015; Fenn-Moltu et al., in review). Nevertheless, the notion that plants and plant products are the dominant invasion pathway for Lepidoptera is consistent with other studies that indicate plant imports as the dominant pathway for introduction of foliage-feeding insects (Kiritani & Yamamura, 2003; Kenis, Rabitsch, Auger-Rozenberg & Roques, 2007; Liebhold et al., 2012). A few families (e.g., Erebidae, Cossidae, Sphingidae) were frequently associated with non-plant products such as machinery/electrical commodities, mineral products and stone/glass commodities (Figure 6). These associations most likely reflect the tendency of species in these families to be transported in the "hitchhiking" pathway – i.e. transported with inanimate objects (Kiritani & Yamamura, 2003; Toy & Newfield, 2010; Gippet, Liebhold, Fenn-Moltu & Bertelsmeier, 2019; Meurisse, Rassati, Hurley, Brockerhoff & Haack, 2019). The hitchhiking pathway may be particularly common for species that have behaviours that associate certain life stages (eggs, pupae) with non-host material – e.g., *Lymantria dispar* eggs are often laid on non-host material such as vehicles, machinery and shipping containers (Paini, Mwebaze, Kuhnert & Kriticos, 2018).

Generalists appear to be more successful invaders than species with a narrow food spectrum, especially on islands, where detritivores and stored food pests are frequently over-represented. There would thus be benefits from biosecurity measures that target exclusion of such generalist detritivores. However, micromoths, often with small, concealed-feeding larvae, may be easily overlooked during border inspections and thus may be difficult targets for border biosecurity actions.

Acknowledgements

Conflict of Interest Statement

The authors declare no conflict of interest.

Data availability statement

The data of non-native, established Lepidoptera species is part of a larger database, "International Non-native Insect Establishment Data", which is periodically updated and freely available on Zenodo via https://doi.org/10.5281/zenodo.5245301 (Turner, Blake & Liebhold, 2021). The datasets from Supplements S2–S5 and S7–S9 are available on Dryad (https://doi.org/10.5061/dryad.31zcrjdnw).

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Biosketch

Our research team focuses on the global distribution of non-native insect species, their diversity, systematics, biogeographic patterns, host specificity and socioeconomics drivers. The team is organised as working groups, "Global Socioeconomic drivers of insect invasions" at the National Socio-environmental Synthesis Center and "Reconstructing Global Insect Invasion Dynamics" at the Czech University of Life Sciences.

Author contributions: RM and AML conceived the ideas; all authors collected the data; RM, RMT, REB, TY and AML analysed the data; all authors contributed to the writing, led by RM and AML.

Supplementary files

are available at:

https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fjbi.14393&file=jbi14393-sup-0001-Supinfo.zip

Supplement S1 Sampled regions and data sources for non-native established species (Figure S1, Table S1) and total Lepidoptera species (Table S1), interception data (Figure S2, Table S2), and commodities data (Figure S3, Table S3), including respective references.

Supplement S2 Numbers of total species pooled to Lepidoptera families in the 11 investigated regions, and global number of species per family (column "world").

Supplement S3 Numbers of established non-native species for each Lepidoptera family in the 11 investigated regions, and total number of unique established species per family pooled across the 11 regions (column "total").

Supplement S4 Numbers of intentionally introduced species pooled to Lepidoptera families in the 11 investigated regions, and total number of unique intentionally introduced species per family pooled from the 11 regions (column "sum_intent").

Supplement S5 List of species established in the 11 investigated regions, including intentionally introduced species (column "intentional_release" = yes).

Supplement S6 Statistics of the species–area relationships in the 11 investigated regions as illustrated in Figure 2; log-log species–area relationships (Figure S6) in the 11 investigated regions for the 14 of the top-16 families not illustrated in Figure 2.

Supplement S7 Numbers of interceptions and of intercepted species of Lepidoptera (pooled to family) at ports of entry pooled from mainland USA, Hawaii, Canada, EPPO, UK, Japan, South Korea, South Africa, Australia and New Zealand.

Supplement S8 Numbers of commodity interceptions pooled to Lepidoptera families with at least 100 interceptions, recorded from 14 classes of trade commodities: plant products, animal products, wood products, foodstuffs, transport, metal products, machinery/electrical products, mineral products, stone/glass, chemical products, plastics/rubber, textiles, footwear/headgear, and miscellaneous. Interceptions are pooled from USA incl. Hawaii, Canada, EPPO, Japan, Australia and New Zealand.

Supplement S9 Numbers of commodity interceptions from plant commodities subset, itemised to 10 sub-classes: cereals (HS-10), coffee/tea/spices (HS-09), flours (HS-11), fruit/nuts (HS-08), gum/resin (HS-13), live plants/cut flowers (HS-06), vegetable fibres (HS-53), seeds/grains/medicinal (HS-12), vegetable products (HS-14), vegetables (HS-07). Numbers are pooled to the same Lepidoptera families as in Appendix S8.

Supplement S10 Results from Figures 1–5 for non-native established species *including* intentionally introduced species.