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Alien insect dispersal mediated by the global movement of commodities

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Abstract

Globalization and economic growth are recognized as key drivers of biological invasions. Alien species have become a feature of almost every biological community worldwide, and rates of new introductions continue to rise as the movement of people and goods accelerates. Insects are among the most numerous and problematic alien organisms, and are mainly introduced unintentionally with imported cargo or arriving passengers. However, the processes occurring prior to insect introductions remain poorly understood. We used a unique dataset of 1,902,392 border interception records from inspections at air, land and maritime ports in Australia, New Zealand, Europe, Japan, the United States of America and Canada to identify key commodities associated with insect movement through trade and travel. A total of 8,939 species were intercepted, and commodity association data were available for 1,242 species recorded between 1960 and 2019. We used rarefaction and extrapolation methods to estimate the total species richness and diversity associated with different commodity types. Plant and wood products were the main commodities associated with insect movement across cargo, passenger baggage and international mail. Furthermore, certain species were mainly associated with specific commodities within these, and other broad categories. More closely related species tended to share similar commodity associations, but this occurred largely at the genus level rather than within orders or families. These similarities within genera can potentially inform pathway management of new alien species. Combining interception records across regions provides a unique window into the unintentional movement of insects, and provides valuable information on establishment risks associated with different commodity types and pathways.

Key words

*Commodity trade, globalization, human-mediated dispersal***,** *insects, introduction pathways, invasion risk*

Introduction

The globalization of human activities facilitates species dispersal across historical biogeographic barriers, such that alien species are now an established part of almost every biological community worldwide (Convention on Biological Diversity, 2001). As the international movement of people and goods accelerates and expands, the rate of new introductions continues to rise (Levine and D'Antonio, 2003; Seebens *et al.*, 2017). Some species that are introduced and overcome biotic and abiotic barriers to establishment (Blackburn *et al.*, 2011) cause harmful ecological or economic impacts in their new range (Pagad *et al.*, 2015). In terrestrial ecosystems, insects are among the most numerous and problematic alien organisms, costing at least 70 billion US$ per year globally (Bradshaw *et al.*, 2016; Diagne *et al.*, 2021). Unlike most alien vertebrates and plants, insects are usually introduced unintentionally (Rabitsch, 2010). This typically occurs through the transport of commodities, either because the commodity is their natural host or their immediate environment (contaminant pathway), or because insects have actively attached to an object not directly related to their natural environment (hitchhiking pathway) (Gippet *et al.*, 2019). Introduction pathways encompass the suite of processes that transport a species from one location to another, including both the vector and the human activity resulting in an introduction (Genovesi and Shine, 2004; Pyšek *et al.*, 2011).

Managing introduction pathways and corresponding commodities is therefore a potentially powerful strategy for preventing new introductions, and thus reducing negative impacts on biodiversity, human health (Pyšek and Richardson, 2010; Mazza *et al.*, 2014; Pratt, *et al.*,

2017) and economies (Bradshaw *et al.*, 2016). Risk assessment strategies for alien species often prioritize identifying sources and pathways of introduction (Hulme *et al.*, 2008). Yet when assessing establishment risks and mitigation measures, it may be more efficient to consider the size and composition of species pools moved along particular pathways, rather than focusing on individual species (Brockerhoff *et al.,* 2014). The greater the number of species introduced to a location (colonization pressure), the more species we should expect to establish self-sustaining populations there (Lockwood *et al.*, 2009; Blackburn *et al.*, 2020). Similarly, the number of species transported via a given pathway or commodity is likely closely related to the introduction risk associated with such movement. While progress has been made towards understanding human-mediated dispersal of certain taxa (for example Suarez *et* al., 2005; Brockerhoff *et al.*, 2006; Ward *et al.*, 2006; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019), a global analysis of unintentional insect introduction pathways is lacking. Identifying commerce that transports a wide range of insects worldwide would improve our ability to monitor and manage key pathways, particularly in regions with fewer resources available.

The exact pathways responsible for historical species introductions are usually unknown, but alien species databases and inventories often assign species to the most likely pathway based on their ecology and the assumptions of the assessor (Kenis *et al.*, 2007; Essl *et al.*, 2015; Pergl *et al.*, 2017). However, many countries perform inspections of trade goods, mail and personal baggage at ports of entry (i.e. land borders, air and sea ports and transitional facilities) as part of national biosecurity programmes (Saccaggi *et al.*, 2016; Black and Bartlett, 2020). Due to the large volume of trade, it is only possible to inspect a small fraction of imports (Natural Research Council, 2002). Therefore, inspections are typically not a primary method for excluding arrivals of potential pest species. However, inspection plays a key role in national biosecurity programs as a method for monitoring the presence of organisms in various pathways. This information is of great value in identifying invasion risks, setting phytosanitary policies (e.g. import bans and mandatory phytosanitary treatments) and monitoring compliance with existing import regulations (Sequeira and Griffin, 2014; IPPC Secretariat, 2021). Countries vary in their sampling methods, identification abilities, and the species and commodities they target (Whattam *et al.*, 2014; Turner *et al.*, 2021). Nonetheless, border interception records provide a unique window into the unintentional movement of insects and the commodities they are associated with.

In this study we combined interception records from six regions distributed across four continents to provide the first comprehensive overview of insect-commodity associations in international trade and travel. Most studies of insect commodity associations have considered specific groups (e.g. taxa or feeding groups) of insects arriving in a single country, often on a pre-selected suite of commodities. Bark- and wood-boring insects (e.g. Haack, 2006; Messiner *et al.*, 2008; Roques, 2010; Liebhold *et al.*, 2012; Lawson *et al.*, 2018; Meurisse *et al.*, 2019; Krishnankutty *et al.*, 2020), agricultural pests (e.g. Caton *et al.*, 2006; McCullough *et al.*, 2006; Kenis *et al.*, 2007; Smith *et al.*, 2007; Areal *et al.*, 2008; DeNitto *et al.*, 2015) and ants (e.g. Suarez *et al.*, 2001; Ward *et al.*, 2006; Suhr *et al.*, 2019; Yang *et al.*, 2019; Lee *et al.*, 2020) have been targeted in particular, likely due to the damage to forestry, agriculture and infrastructure that these taxa can cause (e.g. Jetter *et al.* 2002; Aukema *et al.*, 2011; Bradshaw *et al.*, 2016; Paini *et al.*, 2016). In addition to using a standardised system for commodity classification, the broad taxonomic and geographic coverage of interceptions in this study could potentially improve efforts to make predictions about insect introduction pathways. Our aims are to: 1) quantify the richness and diversity of insect species transported with relevant commodities, and 2) ascertain whether commodity associations vary among pathways (e.g. cargo vs. baggage vs. mail), 3) determine if key commodities vary among insect species, and groups of species, and 4) evaluate whether commodity associations are related to insect phylogeny.

Methods

Data acquisition and cleaning

We analysed records of insects detected during inspections of international air and sea cargo, mail, vessels and passenger baggage at ports of entry**.** The data consist of interceptions at air, land and maritime ports from 1960 to 2019 in Australia, New Zealand, member countries of the European and Mediterranean Plant Protection Organisation (EPPO), Japan, the United States of America, and Canada. As the number of individuals detected is not recorded in most regions, each interception represents a single arrival event per species. The insects discovered are destroyed, so while interceptions can be considered a proxy for species' unobserved arrival, they do not directly represent introductions. We included only interceptions between 1960 and 2019 for the years where records where available in each region (Appendix S1: Table S1), where the insect was identified to species level, with information available on the associated commodity. This timeframe corresponds to a period of increased globalization and trade openness (Baldwin and Martin, 1999; Klasing and Milionis, 2014; Feenstra *et al.*, 2015). For most analyses, interceptions of genera with no members identified to species level were also included, as they represent at least one additional species.

We standardized insect taxonomic names across years and recording regions according to the Global Biodiversity Information Facility (GBIF) backbone taxonomy (GBIF Secretariat, 2019) using the taxize (Chamberlain and Szocs, 2013) and rgbif R packages (Chamberlain *et al.*, 2021). GBIF has good coverage of insect taxonomy. While the taxonomic names are not always the most recent, we prioritized standardising to unique genus-species names. The process was largely automated, but occasional unmatched species were corrected manually and a small proportion of synonyms may still be present.

We standardised commodity descriptions using the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods (World Customs Organization, 2021) and subsequently grouped commodity codes into broad classes based on the type of product (Appendix S1: Figure S1). The HS is a hierarchical system of six-digit codes, where the first two digits (HS-2) identify the chapter goods are classified in (e.g. 08: Fruit and nuts, edible; peel of citrus fruit or melons). Some level of misclassification due to manual errors may remain. Standardised classification based on HS codes provides commodity descriptions that can easily be integrated with trade data, and facilitates comparisons across countries and among studies. All analyses were conducted at the level of HS-2 codes or broad commodity classes.

Pooling data across interception regions

There are regional differences in inspection methods and targets, the sources, volume and nature of imports, and the years covered (Appendix S1: Table S1, Turner *et al.*, 2021). However, the main commodity types associated with insects are similar across all regions, with the majority being plants, wood, and related products (Appendix S1: Figure S2). To test if species share similar commodity associations across regions despite the differences, we analysed the 59 species intercepted more than 20 times in two or more regions. We included a separate commodity profile for each region in which a species was intercepted. We used a partial constrained correspondence analysis (CCA) in the vegan package (Oksanen *et al.*, 2019) to estimate the variance in commodity associations explained by species, once the effect of interception region is removed. A CCA relates a matrix of species' abundance or occurrence to a matrix of explanatory variables. Partial CCA is an extension of this method where you can control for the influence of conditioning variables in an additional matrix (Legendre and Legendre, 2012). Pooling the interception records across countries allows us to analyse insect arrivals based on a much wider range of taxa and commodities, and to generalize across regions. As there was an overall similarity in the commodities recorded, and species shared similar commodity associations across regions, we pooled the data for further analysis.

Estimating species richness and diversity

We used rarefaction and extrapolation methods to estimate total species richness (i.e. the number of species intercepted) and species diversity (i.e. the number and relative abundance of species) associated with different commodities, using the iNEXT package (Hsieh *et al.,* 2016). The ChaoRichness() function estimates the asymptote of rarefaction and extrapolation curves and the associated confidence intervals based on the methods proposed in Chao (1984, 1987), giving a conservative lower bound for undetected species richness. Shannon's diversity index considers both the number of species (richness) and their relative abundance (evenness), which helps to distinguish between commodities where species are transported with a similar frequency, and commodities where only a few species are commonly intercepted. The ChaoShannon() function estimates Shannon diversity based on the method proposed by Chao *et al.* (2013). In addition to the commodity type, the pathway a commodity arrives through is likely to influence which species have the opportunity to be transported. The relevant pathway was recorded for most interceptions in Australia and the USA. Only interceptions classed as cargo, passenger baggage or international mail were comparable between the two countries. We estimated the species richness and Shannon diversity associated with commodities in each of these pathways as above. To compare the differences in taxonomic composition we carried out a PERMANOVA using the adonis2() function with Bray-Curtis distances in the vegan package (Oksanen *et al.*, 2019) for orders intercepted with the five commodity classes found in all three pathways (Fig. 1).

<u>Phylogenetic signal of commodity associations</u>

Phylogenetic signal can be defined as the tendency for related species to resemble each other more than they resemble species drawn at random from the tree (Bloomberg & Garland, 2002). To test whether related species share similar commodity associations, we created a tree based on the taxonomic structure of species using the as.phylo() function in the ape package (Paradis and Schliep, 2018), adding branch lengths with the compute.brlen() function. We combined the taxonomic tree with each species' coordinates from the CA, and tested for phylogenetic signal using Abouheif's Cmean in the phylosignal package (Keck *et al.*, 2016). The Cmean index was compared to the null hypothesis that the trait values are randomly distributed in the taxonomy (Keck *et al.*, 2016). Molecular time estimates in Timetree.org (Kumar *et al.*, 2017) represent a synthesis of published divergence time estimates (Hedges *et al.*, 2015). We created an additional phylogenetic tree for the 150 species with available molecular time estimates (Appendix S1: Table S2), and tested for a phylogenetic signal to commodity associations as above.

We used three separate CCAs in the vegan package (Oksanen *et al.*, 2019) to determine at what taxonomic level species share similar commodity associations, and the degree of variance explained by higher taxonomic levels. For each analysis of species "commodity profiles", species' order, family, or genus was the single constraining variable. Taxa including only a single species were excluded from these analyses. The statistical significance of each model was assessed using a permutation test for CCA in the same package.

Correspondence analysis and hierarchical clustering

To explore the relationship between species and the commodities they are transported with, we carried out a correspondence analysis (CA) using the ade4 package (Dray and Dufour, 2007). We calculated the proportion of interceptions on each HS-2 commodity group for each species, in order to compare their "commodity profiles" using the relative number of interceptions per commodity. Species with less than 20 interceptions were excluded as this provides insufficient replication to characterize commodity associations. There were 1,242 species intercepted a sufficient number of times for analysis. The first eight axes of the CA were retained. We used a hierarchical agglomerative clustering analysis in the cluster package (Maechler *et al.*, 2019) to identify species associated with similar suites of commodities. Species were clustered based on their coordinates in the CA, using the agnes() function with Ward's clustering method (Kaufman and Rousseeuw, 1990). We used the permutation test introduced by Greenacre (2011) to determine whether non-random levels of clustering were present, and if so, to indicate at which level the resulting tree can be cut to give the optimal number of clusters. All analyses were conducted in R (R Core Team, 2017) and figures produced using the ggplot2 package (Wickham, 2009).

Results

The dataset comprised 1,902,392 interception events, representing commodity associations for 7,231 species and 1,708 additional genera with no members identified to species level. The species intercepted were mainly Coleoptera (3165 species), Hemiptera (2708 species) and Lepidoptera (1103 species), but also included members of 19 other insect orders. Insects were intercepted on 80 different HS-2 commodity groups, belonging to 14 different commodity classes (Appendix S1: Table S3). With the interception region included as a conditioning variable, species explained 46.7 % of the variance in commodity associations, while the interception region explained just 12.3 % of the variance in commodity associations. Both variables explained significantly more variance than expected by chance (permutation test for CCA with 999 permutations, interception region: $F = 4.15$, $p = 0.001$, species: $F = 1.44$, $p = 0.001$).

Plant products (see Table 1 for description of commodity groups) transported by far the most species, followed by wood products, stone and glass, and machinery and electricals. Textiles were associated with much lower species richness, but transported the highest insect diversity. Animal products and foodstuffs showed similar patterns (Fig. 2). Within the broad categories of plant products and wood products, the HS-2 commodities transporting the greatest species richness were live plants and cut flowers (HS 06), fruit and nuts (HS 08), vegetables (HS 07), wood and articles of wood (HS 44), and coffee, tea, herbs and spices (HS 09). Vegetable fibres (HS 53), plaiting materials (HS 46) and vegetable products and bamboo (HS 14) transported a high diversity of insects relative to species richness (Fig. 3).

While plant products and wood products were associated with the highest richness and diversity across all three pathways (Appendix S1: Figure S5), there were some differences for HS-2 commodities within these categories (Appendix S1: Figure S6). Wood and articles of wood (HS 44) transported the greatest number of species through mail, whereas in passenger baggage live plants and cut flowers (HS 06), wood and articles of wood (HS 44), fruit and nuts (HS 08), vegetables (HS 07) and coffee, tea, herbs and spices (HS 09) all transported high numbers of species (Appendix S1: Figure S6). These same commodities were important in cargo, with the most species associated with live plants and cut flowers (HS 06), and fruit and nuts (HS 08). Wood and articles of wood were associated with the greatest insect diversity in all three pathways (Appendix S1: Figure S6). The exact species intercepted on the same commodity types varied between cargo, baggage and mail (Appendix S1: Figure S4). However, while the commodity class had a significant effect on the taxonomic composition of insects (PERMANOVA with 9999 permutations, $F = 2.48$, $p = 0.01$), we found no significant effect of pathway (PERMANOVA with 9999 permutations, $F = 0.58$, $p = 0.83$).

Commodity associations were non-randomly distributed among species, showing a phylogenetic signal both for the tree with relatedness based on taxonomy (Abouheif's Cmean 0.21 – 0.52, $p = 0.001$), and for the subset of species with information available on phylogenetic divergence times (Abouheif's Cmean 0.23 – 0.49, $p = 0.001$). The genus a species belongs to explained 44.3 % of the variance in species' commodity associations, while family explained 26.3 % and order explained just 6.7 % (see Appendix S1: Table S4 for regional differences). All three taxonomic levels explained significantly more variance than expected by chance (permutation test for CCA with 999 permutations, genus: $F = 2.47$, $p = 0.001$, family: $F = 3.61$, $p = 0.001$, order: $F = 9.64$, $p = 0.001$).

We found 11 distinct clusters of species transported with similar suites of commodities (Fig. 4). The first cluster consisted of 465 species most frequently intercepted with live plants and cut flowers (HS 06), but which were also frequently associated with fruit and nuts (HS 07). These species belong to the orders Hemiptera, Coleoptera, Lepidoptera, Thysanoptera, Hymenoptera, Diptera, Orthoptera, and Dermaptera, in decreasing order of species richness. The second cluster contained 64 species of Coleoptera, Lepidoptera, Hemiptera, Thysanoptera, Diptera, and Hymenoptera, which were most frequently intercepted with vegetables (HS 07). The third cluster was most often transported with ceramics (HS 69) and wood and articles of wood (HS 44), and consisted of 51 species of Coleoptera, Hymenoptera, Hemiptera, Lepidoptera, Blattodea, Orthoptera and Diptera. The fourth cluster of 53 species of Hemiptera, Coleoptera, Orthoptera and Lepidoptera were most frequently transported with ceramics (HS 69). The fifth cluster contained 107 species of Coleoptera, Hemiptera, Hymenoptera, and Lepidoptera which were mainly associated with wood and articles of wood (HS 44). The sixth cluster consisted of 23 species of Hymenoptera, Lepidoptera, Diptera, Coleoptera, Blattodea, Orthoptera and Hemiptera, which were most frequently transported with machinery (HS 84). The seventh cluster consisted of 89 species most frequently transported with coffee, tea, herbs and spices (HS 09), belonging to the orders Hemiptera, Thysanoptera, Lepidoptera, Coleoptera and Diptera. The eighth cluster consisted of 180 species of Hemiptera, Coleoptera, Thysanoptera, Lepidoptera, Diptera, Hymenoptera and Dermaptera, which were most often associated with fruit and nuts (HS 08). The ninth cluster of 162 species were most frequently associated with live plants and cut flowers (HS 06), and belonged to Hemiptera, Coleoptera, Lepidoptera, Diptera, Orthoptera, Thysanoptera, Hymenoptera and Blattodea. The tenth cluster consisted of 39 species of Coleoptera, Psocodea, Blattodea, Zygentoma, Hymenoptera, Lepidoptera and Hemiptera, and were most often intercepted with vegetable products and bamboo (HS 14). The eleventh cluster consisted of just nine species of Coleoptera and Diptera, most frequently associated with meat and crustacean preparations (HS 16). See Appendix S1: Figure S3 for more detail.

Discussion

The establishment of intentionally introduced organisms can be managed through regulations limiting importation and possession. However, prevention of unintentionally introduced organisms is more complex. It is first necessary to identify the major pathways by which these organisms are introduced, which individual national biosecurity agencies typically accomplish via pathway risk analyses (Essl *et al.*, 2020; Hulme, 2009). We pooled border interception records spanning four continents to improve our knowledge of the commodities responsible for unintentional insect introductions. We found that plant and wood products were the dominant means of movement through international trade and travel. While this is well-known for specific insect groups (e.g. Kiritani & Yamamura, 2003; Roques, 2010; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019), our results highlight the wide range of taxa transported with these commodity types. Plant products and wood products were associated with the highest species richness in cargo, in international mail and in passenger baggage, supporting their status as important targets for management across pathways. However, these were not the main commodities transporting all insect species, and many species were primarily associated with distinct commodity groups within these broad categories. This suggests that detailed information about relevant commodities is required for preventing the introduction of specific insect taxa.

The movement of plants and wood have long been recognized as important pathways for insect invasions (Kiritani & Yamamura, 2003; Roques, 2010; Liebhold *et al.*, 2012; Meurisse *et al.*, 2019). National biosecurity programs direct considerable effort towards limiting the accidental movement of insects through quarantine, inspection, mandatory phytosanitary treatments and other extensive pre-border measures (Sequeira and Griffin, 2014), harmonized by the International Plant Protection Convention and other bodies (Hulme 2011). We found that live plants and cut flowers, fruit and nuts, wood and articles of wood, vegetables, and coffee, tea, herbs and spices, in particular transport a high number of species. While there is considerable variation in the insect taxa and commodity types considered in the literature, the importance of live plants (Liebhold *et al.*, 2012; Eschen *et al.* 2015; Meurisse *et al.*, 2019), cut flowers (Work *et al.*, 2005; McCullough *et al.*, 2006; Roques and Auger-Rozenberg, 2006; Kenis *et al.*, 2007; Areal *et al.*, 2008; Hong *et al.*, 2012; Lee *et al.*, 2016; Suhr *et al.*, 2019), wood packaging material (Brockerhoff *et al.*, 2006; Haack, 2006; Messiner *et al.*, 2008; Lawson *et al.*, 2018; Krishnankutty *et al.*, 2020), fruits and vegetables (Work *et al.*, 2005; McCullough *et al.*, 2006; Roques and Auger-Rozenberg, 2006; Kenis *et al.*, 2007; Lee *et al.*, 2016; Suhr *et al.*, 2019) and seeds (McCullough *et al.*, 2006; Kenis *et al.*, 2007; Franić *et al.*, 2019) have been recognised previously. With the addition of coffee, tea, herbs and spices as key plant products, our results support that these commodities are major sources of insect introductions worldwide.

While the same commodity types were generally important across pathways, the species richness and diversity associated with specific HS-2 commodity groups varied (Appendix S1: Figure S6). The taxonomic composition of species associated with a commodity also differed between pathways, for example proportionally more Hemiptera were associated with wood products in cargo than in baggage or mail. Commodities are often subject to different production and pest management practices depending on the pathway. Pathways also necessarily differ in the exact type, volume, treatment, and transport time of commodities, which in turn filters which species are present. For example, fresh fruits imported as commercial cargo typically undergo stringent care during production, and sometimes mandatory phytosanitary treatments to reduce pest risk. Fresh fruits arriving in baggage, on the other hand, may not have been commercially produced, and are controlled through inspection alongside public messaging. Pathway-specific variation in pest management practices during the production, transport and arrival of commodities are likely to strongly influence which species are encountered during inspections.

The movement of textiles (Caton *et al.*, 2006), and abiotic commodities like machinery and building materials (McCullough *et al.*, 2006), containers and used vehicles (Brockerhoff *et al.*, 2006; Ward *et al.*, 2006), and tiles (Work *et al.*, 2005; Haack, 2006) have also been identified as important pathways for insect introductions. Ordination largely separated biotic commodities like plant products and foodstuffs from wood products, and various abiotic commodities based on the associated species (Fig. 4). The similarity in species associated with wood products and abiotic commodities may be due to the presence of wood packaging materials during transport. Up to 70 % of all goods traded internationally (USDA cited in Eyre *et al.*, 2018) are accompanied with some form of wood packaging, which offers a suitable substrate for many insect contaminants and hitchhikers. We are unable to distinguish between species transported with the packaging or the commodity itself based on the interception records, so the associated risk could also stem from the packaging. However, infestation rates of wood packaging materials are low (e.g., 0.17 to 0.25% in the United States prior to ISPM15 (Haack *et al.* 2014)) and are unlikely to be a significant proportion of the records we assess here. We also found that textiles transport a particularly high diversity of insects relative to species richness, along with animal products and foodstuffs. It's likely that many species are only rarely associated with a given commodity, and due to the lower propagule pressure will be less likely to establish (Kolar and Lodge, 2001; Lockwood *et al.,* 2005). Commodities such as textiles where species are more evenly transported may be sources of increased introduction risk.

However, a greater number of species introductions does not necessarily translate into greater impacts. National Plant Protection Organizations rely on species-specific risk assessments to predict the potential damage caused by insects known to be associated with particular commodities. It should also be noted that during the period from which we sourced data (1960-2019), there has been considerable progress in implementation of new biosecurity practices that have likely reduced rates of commodity contamination and total numbers of species entering. For example, the harmonized international standard ISPM-15 established by the International Plan Protection Convention specifies phytosanitary treatments for wood packaging, and has resulted in a substantial decrease in levels of wood-boring insects present in this material (Haack et al. 2014). As another example, during this period the US Department of Agriculture has phased in new quarantine procedures for live plant imports that prohibit importation of plants in a large number of genera until risk analyses can be performed (USDA, 2021). Thus, numbers of species associated with commodities likely changed during the period from which our data was sourced.

Prevention strategies that focus on high-risk pathways alongside quarantine protocols targeting individual taxa are crucial for limiting arrivals of new and damaging species (e.g. Keller *et al.*, 2009). Aichi Biodiversity Target 9 aimed that "by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment" (Convention on Biological Diversity, 2010). This clearly remains a work in progress (e.g. Tittensor *et al.*, 2014), and continued research into pathway identification and management is necessary. Economic analyses are needed to evaluate whether the costs of additional biosecurity controls are smaller than the benefits of preventing invasions (Welsh *et al.*, 2021). Moreover, future work could improve our estimates of species richness and diversity associated with different commodities by adjusting for import volume. The species contaminating or hitchhiking with a commodity are necessarily a subset of the species present in the region it originated from, or potentially from intermediate stops along the way.

Comparing the size and composition of species pools arriving from different world regions alongside associated trade volumes would help further explain patterns of introduction risk. We also observed that the degree of diversity in commodity associations varied considerably between taxa. Quantifying this variation would help to adjust the level of detail required for risk assessments and predictive modelling of different insect groups.

Species intercepted during port-of-entry inspections represent only a small proportion of the pool of insects arriving in a region (Kenis *et al.*, 2007), and many species which arrive infrequently are likely never detected (Brockerhoff *et al.*, 2014). The exact pathways of many new introductions are therefore unknown, and we may not have extensive knowledge about the commodities they are transported with. On condition that related insects tend to be transported with similar suites of commodities, species with known commodity associations could provide clues to the dispersal pathways of their more poorly observed relatives. Our results show that related species do to some extent share similar commodity associations, although there remains a lot of variation within insect taxa and interception regions. The similarities in commodity associations within genera could supply valuable information for targeting pathway management of new species.

Interceptions provide direct evidence of an association between an organism and a commodity, but come with a number of limitations. Inspections often focus on commodities and pathways that *a priori* are considered high-risk, and may preferentially, or exclusively, record interceptions according to lists of regulated goods or regulated pest species (Eschen *et al.*, 2015). As the movement of plant and wood products are recognised as major pathways of insect introductions, they may be more frequently targeted for inspection. The greater intensity of inspections may thus lead to more interceptions irrespective of actual risk, creating a feedback to targeting of these commodities. It is difficult to correct for inspection effort as practices vary between countries and pathways, and are adapted over time as risk assessments are updated, or new biosecurity policies come into force. Additionally, our analyses focus on records identified to species level, and might not be representative of less easily identifiable taxa. While our results are based on insects arriving in six different regions, these are high-income countries and may not be representative of introductions to many developing nations. Unfortunately, negative inspections were not recorded. Randomized, statistically sound inspection systems such as the USDA Agricultural Quarantine Inspection Monitoring system (USDA, 2011) would provide greater power to quantify pathway risks when comparing and combining interception records, but are only focused on a few pathways in a few countries (Griffin, 2020).

The breadth and focus of inspections varies between regions, and alongside differences in import volume, production practices, trade partners, and biosecurity measures, are likely to influence the subset of commodity associations we observe (Saccaggi *et al.*, 2016; Turner *et al.*, 2021). In Europe, economically harmful plant-pests are "black-listed" from entering and being moved around the continent, and interceptions are largely restricted to these quarantine species (European Commission, 2002). Inspectors must check all consignments that could contain quarantine insects, but the exact sampling volumes and methods vary between the European member states (Bacon *et al.*, 2012). Biosecurity programs in Australia and New Zealand operate based on "white-lists" of species that have been assessed and are considered safe (Eschen *et al.*, 2015). However, from New Zealand we only had access to interceptions of ants (Formicidae) and forest insects, with a corresponding bias in associated commodities. In the USA, Canada and Japan, the system is similar to Europe in that they have "black lists" of quarantine pests (Animal and Plant Health Inspection Service, 2020; Canadian Food

Inspection Agency, 2021; Ministry of Agriculture and Fisheries, 2021), but these are generally less restrictive. Records from the USA made up the majority of both interception events and individual species intercepted, and our results were strongly influenced by the commodity associations of insects arriving in the USA (Appendix S1: Figure S7). See Appendix S1: Figures S8-S11 for more detail about regional differences.

Nevertheless, the trends in commodity associations we observed are likely to be widely applicable. We used rarefaction and extrapolation methods to estimate species richness and diversity for standardized sample sizes (Chiarucci *et al.*, 2008), so we expect the ranking of commodities to be robust. While the list of commodities and species transported is almost certainly incomplete (Eschen *et al.*, 2015), the clusters of species associated with distinct commodities are likely to be robust. In most cases, inspection is not an effective method for excluding pest arrival and establishment directly, but provides crucial information for risk assesment. Pooling interception records across regions captures complementary aspects of the human-mediated dispersal of insects, rather than focussing on insects arriving in a single region. The broad range of species and commodities intercepted provide a meaningful overview of the variation in commodity associations between and within taxa, as well as between pathways.

Conclusions

Pathway analysis and management are powerful strategies for predicting and preventing new introductions of contaminant and hitchhiking insects. While knowledge of the exact pathways of unintentional introductions is scarce, pooling interception records across multiple regions provides a unique source of information on relevant commodities. Plant and wood products are important commodities across the cargo, baggage and mail pathways. Live plants and cut flowers, fruit and nuts, wood and articles of wood, vegetables, and coffee, tea, herbs and spices in particular transport a high number of species. Commodities associated with high insect diversity, such as textiles, may be additional priorities for control measures.

While plants, wood and their associated products are important overall, the key targets for pathway management will not be the same for all alien species. Similarities in commodity associations within insect genera may provide valuable information for the management of potential previously unknown invaders. Our results highlight the wide range of commodities that are potential sources of new insect introductions, and the need for detailed information on relevant dispersal commodities to effectively limit future insect introductions.

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Tables

Table 1: Key commodity classes associated with insect movement, and the HS-2 commodity groups belonging to each class.

Commodity class	HS-2 codes	HS-2 codes and full descriptions according to the Harmonized System
Animal products	01 Live animals, 02 Meat, 03 Fish/crustaceans, 04 Dairy/eggs/honey, 05 Animal products, 41 Hides/skins, 42 Leather	01 Animals; live, 02 Meat and edible meat offal, 03 Fish and crustaceans, molluscs and other aquatic invertebrates, 04 Dairy produce; birds' eggs; natural honey; edible products of animal origin, not elsewhere specified or included, 05 Animal originated products; not elsewhere specified or included, 41 Raw hides and skins (other than furskins) and leather, 42 Articles of leather; saddlery and harness; travel goods, handbags and similar containers; articles of animal gut (other than silk-worm gut)
Plant products	06 Live plants/cut flowers, 07 Vegetables, 08 Fruit/nuts, 09 Coffee/ tea/herbs/spices, 10 Cereals, 11 Flours, 12 Seeds/ grains/medicinal plants, 13 Gum/resin, 14 Vegetable products and bamboo, (1111) soil around plants, 53 Vegetable fibres	06 Trees and other plants, live; bulbs, roots and the like; cut flowers and ornamental foliage, 07 Vegetables and certain roots and tubers; edible, 08 Fruit and nuts, edible; peel of citrus fruit or melons, 09 Coffee, tea, mate and spices, 10 Cereals, 11 Products of the milling industry; malt, starches, inulin, wheat gluten, 12 Oil seeds and oleaginous fruits; miscellaneous grains, seeds and fruit, industrial or medicinal plants; straw and fodder, 13 Lac; gums, resins and other vegetable saps and extracts, 14 Vegetable plaiting materials; vegetable products not elsewhere specified or included, (1111) soil around plants, 53 Vegetable textile fibres; paper yarn and woven fabrics of paper yarn
Foodstuffs	15 Oils/fats, 16 Meat/ fish/crustacean preparations, 17 Sugars, 18 Cocoa, 19 Cereal/flour preparations, 20 Vegetable preparations, 21 Food preparations, 22 Beverages/vinegar, 23 Fodder/vegetable residue, 24 Tobacco	15 Animal or vegetable fats and oils and their cleavage products; prepared animal fats; animal or vegetable waxes, 16 Meat, fish or crustaceans, molluscs or other aquatic invertebrates; preparations thereof, 17 Sugars and sugar confectionery, 18 Cocoa and cocoa preparations, 19 Preparations of cereals, flour, starch or milk; pastrycooks' products, 20 Preparations of vegetables, fruit, nuts or other parts of plants, 21 Miscellaneous edible preparations, 22 Beverages, spirits and vinegar, 23 Food industries, residues and wastes thereof; prepared animal fodder, 24 Tobacco and manufactured tobacco substitutes
Wood products	44 Wood/articles of wood, 45 Cork, 46 Plaiting materials, 47 Wood pulp, 48 Paper, 49 Printed matter	44 Wood and articles of wood; wood charcoal, 45 Cork and articles of cork, 46 Manufactures of straw, esparto or other plaiting materials; basketware and wickerwork, 47 Pulp of wood or other fibrous cellulosic material; recovered (waste and scrap) paper or paperboard, 48 Paper and paperboard; articles of paper pulp, of paper or paperboard, 49 Printed books, newspapers, pictures and other products of the printing industry; manuscripts, typescripts and plans

Textiles	50 Silk, 51 Wool, 52 Cotton, 54 Synthetic fabric, 56 Twine/ felt/rope/cables, 57 Carpets, 61 Clothing, knitted, 62 Clothing, not knitted, 63 Textile articles, tents	50 Silk, 51 Wool, fine or coarse animal hair; horsehair yarn and woven fabric, 52 Cotton, 54 Man-made filaments; strip and the like of man-made textile materials, 56 Wadding, felt and nonwovens, special yarns; twine, cordage, ropes and cables and articles thereof, 57 Carpets and other textile floor coverings, 61 Apparel and clothing accessories; knitted or crocheted, 62 Apparel and clothing accessories; not knitted or crocheted, 63 Textiles, made up articles; sets; worn clothing and worn textile articles; rags
Stone/Glass	68 Stone/plaster, 69 Ceramics, 70 Glass	68 Stone, plaster, cement, asbestos, mica or similar materials; articles thereof, 69 Ceramic products, 70 Glass and glassware
Machinery/ Electrical	84 Machinery, 85 Electricals	84 Nuclear reactors, boilers, machinery and mechanical appliances; parts thereof, 85 Electrical machinery and equipment and parts thereof; sound recorders and reproducers; television image and sound recorders and reproducers, parts and accessories of such articles

Figure legends

Figure 1: The taxonomic composition of interceptions on commodities arriving through the baggage, cargo and mail pathways in Australia and the USA. The bars are coloured by the proportion of interception events for each order. Only commodity classes with more than 20 interceptions in all three pathways are shown.

Figure 2: a) The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red) transported with each commodity class, b) the observed (blue), and estimated additional undetected Shannon diversity (red) transported with each commodity class. The error bars indicate the standard error around the estimates of total richness and diversity.

Figure 3: a) The observed species richness (blue) and Chao1 estimates of additional undetected species richness (red), and b) the observed, and estimated additional undetected Shannon diversity transported with each HS-2 commodity group classed as plant products or wood products. The error bars indicate the standard error around the estimates of total richness and diversity.

Figure 4: A *correspondence analysis of species' commodity associations, where a) the HS-2 commodity groups are coloured by the broad commodity class they belong to and the size of the triangles relate to their total contribution to the principal components, b) species are shown as circles coloured by the cluster they belong to, and the HS-2 commodity groups species in each cluster are intercepted on most frequently are labelled, and c) species are shown as circles coloured by the order they belong to.*

Figures

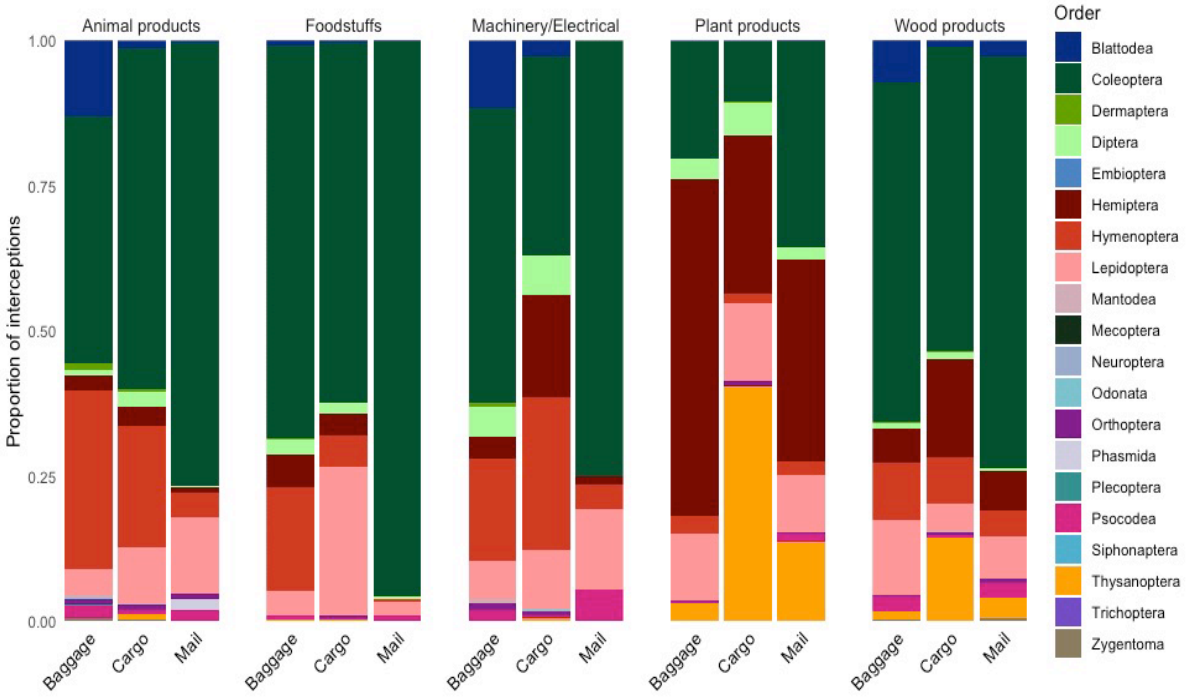

Figure 1

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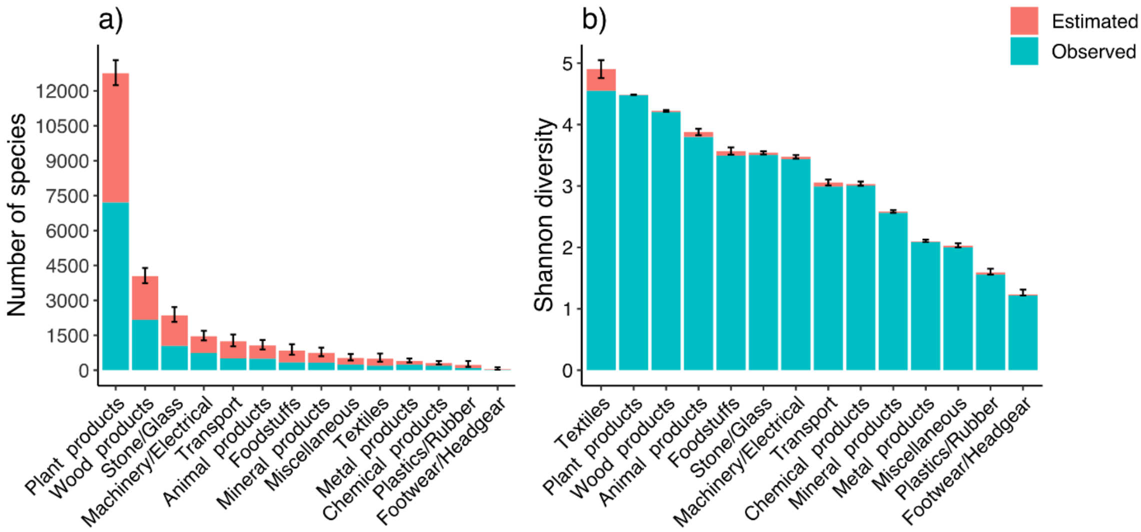
a)
Number of species
12000
10500
9000
7500
6000
4500
3000
1500
0
Plant products
Wood products
Stone/Glass
Machinery/Electrical
Transport
Animal products
Foodstuffs
Mineral products
Miscellaneous
Textiles
Metal products
Chemical products
Plastics/Rubber
Footwear/Headgear
b)
Shannon diversity
5
4
3
2
1
0
Textiles
Plant products
Wood products
Animal products
Foodstuffs
Stone/Glass
Machinery/Electrical
Transport
Chemical products
Mineral products
Metal products
Miscellaneous
Plastics/Rubber
Footwear/Headgear
Estimated
Observed

Figure 2

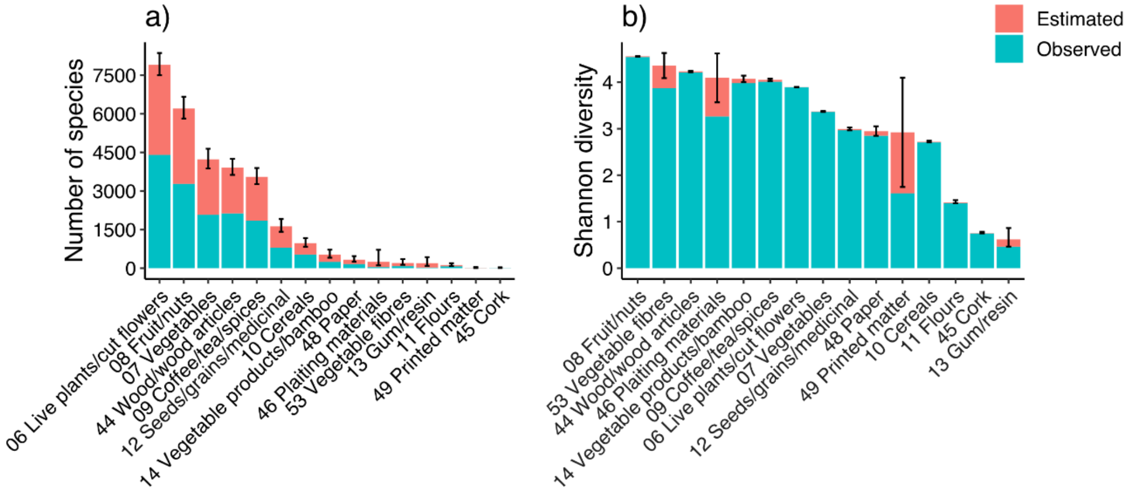
a)
Number of species
7500
6000
4500
3000
1500
0
06 Live plants/cut flowers
08 Fruit/nuts
07 Vegetables
44 Wood/wood articles
09 Coffee/tea/spices
12 Seeds/grains/medicinal
10 Cereals
14 Vegetable products/bamboo
48 Paper
46 Plaiting materials
53 Vegetable fibres
13 Gum/resin
11 Flours
49 Printed matter
45 Cork
b)
Shannon diversity
4
3
2
1
0
08 Fruit/nuts
53 Vegetable fibres
44 Wood/wood articles
46 Plaiting materials
14 Vegetable products/bamboo
09 Coffee/tea/spices
06 Live plants/cut flowers
07 Vegetables
12 Seeds/grains/medicinal
48 Paper
49 Printed matter
10 Cereals
11 Flours
45 Cork
13 Gum/resin
Estimated
Observed

Figure 3

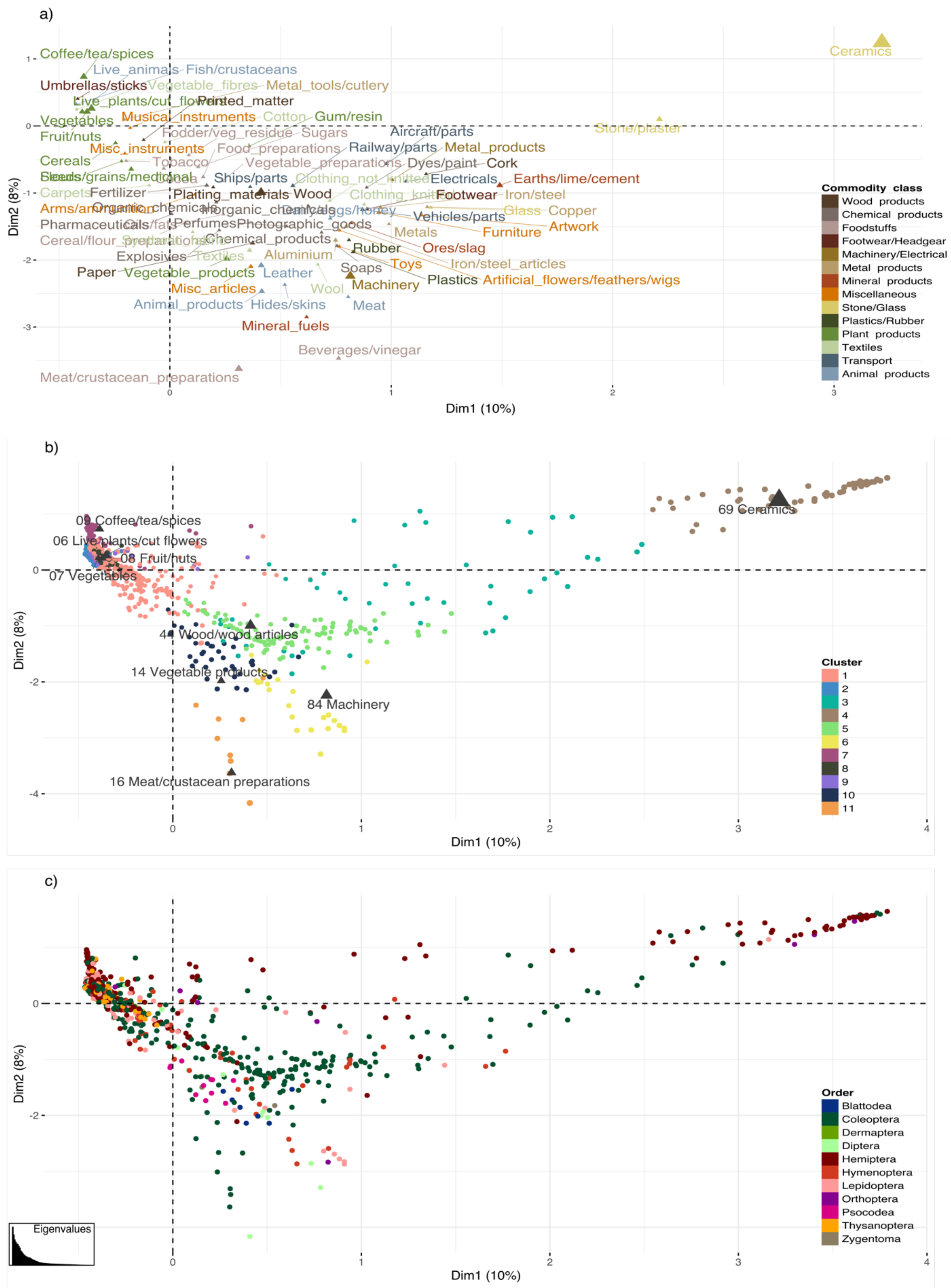
a)
Dim2 (8%)
Dim1 (10%)
Coffee/tea/spices
Live_animals
Fish/crustaceans
Umbrellas/sticks
Vegetable_fibres
Metal_tools/cutlery
Printed_matter
Vegetables
Musical_instruments
Cotton
Gum/resin
Fruit/nuts
Aircraft/parts
Stone/plaster
Ceramics
Fodder/veg_residue
Sugars
Misc_instruments
Food_preparations
Railway/parts
Metal_products
Cereals
Tobacco
Vegetable_preparations
Dyes/paint
Cork
Ships/parts
Electricals
Earths/lime/cement
Carpets
Fertilizer
Plaiting_materials
Wood
Footwear
Iron/steel
Organic_chemicals
Glass
Copper
Pharmaceuticals
Perfumes
Photographic_goods
Vehicles/parts
Artwork
Metals
Furniture
Chemical_products
Explosives
Textiles
Aluminium
Rubber
Ores/slag
Paper
Vegetable_products
Leather
Soaps
Toys
Iron/steel_articles
Misc_articles
Wool
Machinery
Plastics
Artificial_flowers/feathers/wigs
Animal_products
Hides/skins
Meat
Mineral_fuels
Beverages/vinegar
Meat/crustacean_preparations
Commodity class
Wood products
Chemical products
Foodstuffs
Footwear/Headgear
Machinery/Electrical
Metal products
Mineral products
Miscellaneous
Stone/Glass
Plastics/Rubber
Plant products
Textiles
Transport
Animal products
b)
Dim2 (8%)
Dim1 (10%)
09 Coffee/tea/spices
06 Live plants/cut flowers
08 Fruit/nuts
07 Vegetables
69 Ceramics
44 Wood/wood articles
14 Vegetable products
84 Machinery
16 Meat/crustacean preparations
Cluster
1
2
3
4
5
6
7
8
9
10
11
c)
Dim2 (8%)
Dim1 (10%)
Eigenvalues
Order
Blattodea
Coleoptera
Dermaptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Orthoptera
Psocodea
Thysanoptera
Zygentoma

Figure 4