Precise knowledge of commodity trade is needed to understand invasion flows

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Globalization has led to the unintentional movement of thousands of species around the world, necessitating a better understanding of how species are spread by international trade to prevent new invasions. However, to date, the evidence implicating global trade in intercontinental species flows has been mixed. Here, we show that commonly used proxies of global trade, such as general and agricultural imports, fail to explain the invasion flows of alien ants from donor regions to the continental US. Analysis of 97 individual commodity flows revealed instead that plant and fruit imports – a small subset of all agricultural commodities – were primarily associated with invasion flows of ants. The transport patterns of all 95 other commodities, including most "agricultural" commodities, differed from those of alien ants. Our findings highlight the need to determine precisely which commodities serve as introduction pathways for a particular taxon in order to account for invasion flows and identify likely source regions of future invasions in a world of evolving trade relationships.

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Increasing international trade and human movement have resulted in the accidental translocation of thousands of species worldwide at an unprecedented scale. Although many of these species fail to overcome biotic and abiotic barriers to establish outside of their native range, those that do succeed are among the greatest threats to global biodiversity (Mack *et al*. 2000) as they often play key roles in animal extinctions (Clavero and García-Berthou 2005). In addition to impacts on natural ecosystems, invasive species cause damage to physical infrastructure, agriculture, forestry, and human health (Kettunen *et al*. 2009). At present, invasion rates continue to accelerate, and new invasive species are continuously emerging across the planet (Seebens *et al*. 2015).

Although human activity is responsible for the vast majority of biological invasions, most research has focused on the role of habitat or species characteristics affecting invasion success, rather than on human-mediated dispersal (Catford *et al*. 2009). Recent scrutiny of emerging challenges and opportunities in invasion science highlighted globalized trade as among the most important issues requiring further study (Ricciardi *et al*. 2017). Improved understanding of how globalization affects the accidental transport of invasive species is urgently needed because biological theory alone cannot explain current invasions (Kueffer 2017). Previous studies have correlated the number of invasive species per country with different socioeconomic indicators, providing an indication that human activities are linked to the overall level of invasion (Brenton-Rule *et al*. 2016; Dawson *et al*. 2017). However, these are very general proxies of the accidental transport of species, and it remains unclear to what extent they can aid in identifying where new invasions might occur and from where they might originate (Capinha *et al*. 2018). These broad proxies have also been used to assess the relative importance of trade compared to environmental factors in shaping distributions of invasive species. Depending on the study, this has led to the conclusion that trade (or a related socioeconomic proxy) is the most important driver of invasions (Pyšek *et al*. 2010), that trade is an important factor among several others (Capinha *et al*. 2020), or that trade is not linked to invasion patterns at all (Roura-Pascual *et al*. 2011). But determining the importance of trade may depend to a large extent on what metrics are used; that is, the effective use of trade data for understanding or predicting invasions may require prior knowledge about the biology of a particular taxonomic group and its propensity to be associated with different commodities.

Here, we investigated whether invasion flows are linked to general imports, agricultural trade flows, or more detailed commodity categories. To do so, we focused on commodity flows to the US, the world's largest economy and the biggest exporter and importer of goods and services, and therefore a key player in ongoing globalization. Annual trade in agricultural goods, which are particularly prone to host invasive species (Paini *et al*. 2016), exceeds US$260 billion (Kenner and Hui 2020). In the past decade, the US has traded more commodities than ever before (Kenner and Hui 2020), creating opportunities for unintentional species introductions.

More than 11,000 nonnative species (referred to hereafter as "alien" species) are estimated to have become established in the US (Simpson and Eyler 2018). Among these species, ants (Formicidae) are a prominent and particularly well-documented taxon that has often been unintentionally introduced by humans (Holway *et al*. 2002). The complex social structure of ants has contributed to their ecological success as highly invasive species (Bertelsmeier *et al*. 2017). Currently,

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more than 240 ant species are known to have established populations outside of their native range (Bertelsmeier *et al*. 2017). Previous studies using border interception data at ports of entry have suggested that ants are not traveling indiscriminately on any types of goods, but rather are usually transported via fresh fruit and living plants (Suarez *et al*. 2010).

Using flows of alien ant species to the US and flows of general trade, agricultural trade, the plant and fruit trade, and 97 more detailed commodity categories, we examined whether commonly used trade metrics are associated with invasion flows, or if more precise information about the trade in commodities is needed.

Methods

Data

Species distributions

To determine the number of alien ant species that have established in the continental US (that is, the 48 contiguous states plus Alaska), we used the georeferenced database Antmaps (antmaps.org; an authoritative database maintained and updated regularly by experts based on new records in the peer-reviewed scientific literature; Janicki *et al*. 2016). Currently, 98 alien ant species have spread across the continental US and have established at least at one outdoor location worldwide (in order to qualify as "alien species"). One of these species, *Pheidole guineensis*, was excluded from the analyses because its native range is unknown, which prevented the mapping of invasion flows for this species. To calculate the geographic profile representing the "flow" of established ant species from their donor regions to the US, we defined the species' native range as all countries containing native but no introduced populations. For species whose native range encompassed more than one world region, we weighted the flow from each of six world regions (Africa, Asia, Europe, Latin America, Northern America, and Oceania) by the number of political regions where the species was recorded as native (that is, non-overlapping country or subcountry polygons representing states, counties, or islands, all of which are more homogenous in size than entire countries; Janicki *et al*. 2016). The most widespread species are occasionally introduced via bridgehead locations where they are already invasive and do not arrive directly from the native range (Bertelsmeier *et al*. 2018). Therefore, estimated "flows" between the native range of such species and the US may not reflect their actual introduction pathways. To avoid biases due to the bridgehead effect, we excluded the 46 most widespread species, with invaded ranges covering several world regions, from the analyses (WebTable 1).

Trade data

To calculate import flows to the US for different categories of commodities, we used the UN Harmonized Commodity Description and Coding System ("Harmonized System" or HS), an international nomenclature for product classification. The HS comprises approximately 5300 article or product descriptions grouped into 97 broad categories (WebTable 2). Import data (reported in US dollars) for all 97 broad categories of commodities were sourced from the US Census Bureau. We used import data for the 49 continental US states and 229 trade partner countries across the world, summed over the years 1991–2018. Data for this period comprised most of the exchanged commodity volumes since the beginning of the 20th century. We used records of inflation from the World Bank to convert trade records, which were expressed in US dollars for the year 2017. To standardize import profiles of geographic origins for each commodity, we divided imports arriving from each trading partner (in US dollars) by the total value of this commodity import to the US. This allowed representation of the relative contribution of different parts of the world to each commodity flow and avoided assigning greater weight to commodities with high monetary values. General import flows were calculated by summing all 97 individual commodity import flows, and agricultural trade flows were calculated by summing import flows of commodity categories 01–20. We also calculated a "plant and fruit" trade flow – often considered an important pathway for the transport of ants – by combining commodity categories 06, 07, and 08 (WebTable 3).

Statistical analyses

To test whether the flows of general trade, agricultural trade, and plant and fruit trade differed from the flow of alien species to the US, we used chi-square tests with 2000 Monte Carlo replicates to determine *P* values.

Correspondence analysis

To analyze the similarities of import flows of the 97 commodity categories, we performed a correspondence analysis (CA) on the import profiles of geographic origins for all commodity categories, after row standardization (Greenacre and Primicerio 2013). Each row represented the compositional data of import flows for a commodity category, with columns consisting of world regions. Differences among commodity profiles of geographic origins were represented in the two-dimensional space of the factorial map. The first two axes represented 59% of the total inertia. We added profiles of general trade, agricultural trade, and the plant and fruit trade flows, as well as the profile of alien species flows, to the CA space by projecting them as supplementary individuals (that is, additional points that do not determine the axes, but can be plotted on the same factorial map using the same transformation).

Classification

To identify commodity flows that share the same geographic origins, we performed a classification of import profiles using a hierarchical cluster analysis. We first calculated

Ward distances between the coordinates of the commodity categories in the CA space, keeping all five axes. Next, to test how many clusters constituted statistically significant groups among the 97 commodity profiles and four supplementary individuals (general trade, agricultural trade, plant and fruit trade, and alien species flows), we used a simple permutation test (Greenacre and Primicerio 2013) for determining homogeneous clusters of import profiles. This method allowed determination of the presence of nodes in the hierarchical clustering tree with levels lower than would be expected from dendrograms constructed on random permutations of the data. To generate distribution import flows from each world region under the null hypothesis that no differences exist among flows (ie geographic profiles for different commodities), we randomly permuted the data for each world region across commodity profiles (ie we performed column-wise permutations of the rows, where rows corresponded to commodities' profiles and columns corresponded to world regions). The test was performed with 999 permutations. The primary objective of the permutation testing was to define the level at which the tree should be cut in order to obtain non-random levels of homogeneous clustering in the set of profiles.

Results

Ant invasion flows to the US originated predominantly from Latin America and, to a much lesser extent, from Asia and Europe (Figure 1), and differed from general trade flows, which originated predominantly from Asia, followed by Europe, Northern America, and Latin America (χ^2 = 102.38, $P < 0.001$; Figure 1). The results suggest that this commonly used proxy of trade was too general to reflect the origins of ant invasion flows due to the inclusion of many commodities (such as textiles, machinery, or electronics) that are unlikely to serve as pathways for insect introductions. Moreover, general trade flows may give too much weight to countries exporting manufactured products and underrepresent countries exporting fresh products. However, we found that agricultural trade flows also differed from alien species flows, as the former originated to a greater extent from Northern America and Asia (χ^2 = 28.27, $P < 0.001$; Figure 1). This indicates that agricultural trade was also overly general, as it too included irrelevant commodities (such as meat or fish).

Previous analyses of biosecurity inspections at airports and maritime ports indicated that ants are frequently found on plants or fruits (Suarez *et al.* 2005). To test if the plant and fruit trade was associated with ant flows, we calculated trade flows for plants and fruits only, corresponding to the UN Comtrade database commodity categories 06, 07, and 08 (this includes trees and other live plants; bulbs; roots; cut flowers and ornamental foliage; vegetables, edible roots, and tubers; fruits and edible nuts; and peel of citrus fruit or melons). Plant and fruit trade flows did not differ significantly from flows of ants (χ^2 = 3.854, P = 0.54; Figure 1), implying that more precise trade metrics may be necessary to identify associations between trade flows and the geographic origins of alien ants in the US.

However, other commodities may be associated with the flows of alien ants by chance, even if they do not serve as vectors of ants. To test whether other commodity categories were also associated with alien ant flows, we examined the flows of all 97 commodity categories listed by the UN Comtrade database. To analyze similarities among the flows of all 97 commodity categories, we calculated an "import profile" of geographic origins for each commodity category. An import profile for a given commodity category represented the composition of trade flows originating from each of the world regions. Each regional flow consisted of the sum of imports from all countries in a given world region, divided by the total value (in US dollars) of imports of this commodity category in the US. Using this compositional data, we performed a CA on all commodity import profiles. General trade, agricultural trade, plant and fruit trade, and alien ant flows were then projected as supplementary individuals to define their position within the CA factorial space (Figure 2). A hierarchical classification within this factorial space (Greenacre and Primicerio 2013) and a permutation test for clusteredness revealed 14 groups

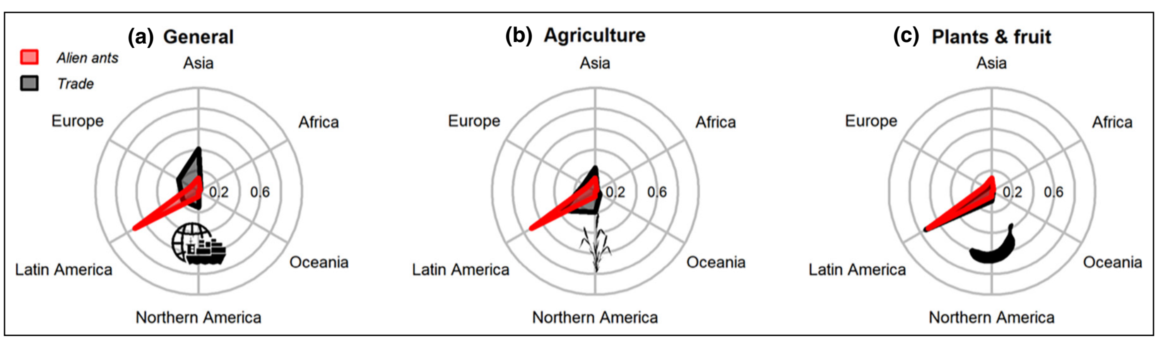

Figure 1. Commodity imports (black polygons) and alien ant flows (red polygons) from donor regions to the US. Each spoke of the radar chart represents the flow originating from one of the six world regions (note: Northern America refers only to the US and Canada, whereas Latin America refers to Mexico, Central America, and South America). The length of a spoke represents the proportion of the flow from one world region over the total import flows. (a) General trade flows, (b) agricultural trade flows, (c) plant and fruit trade flows.

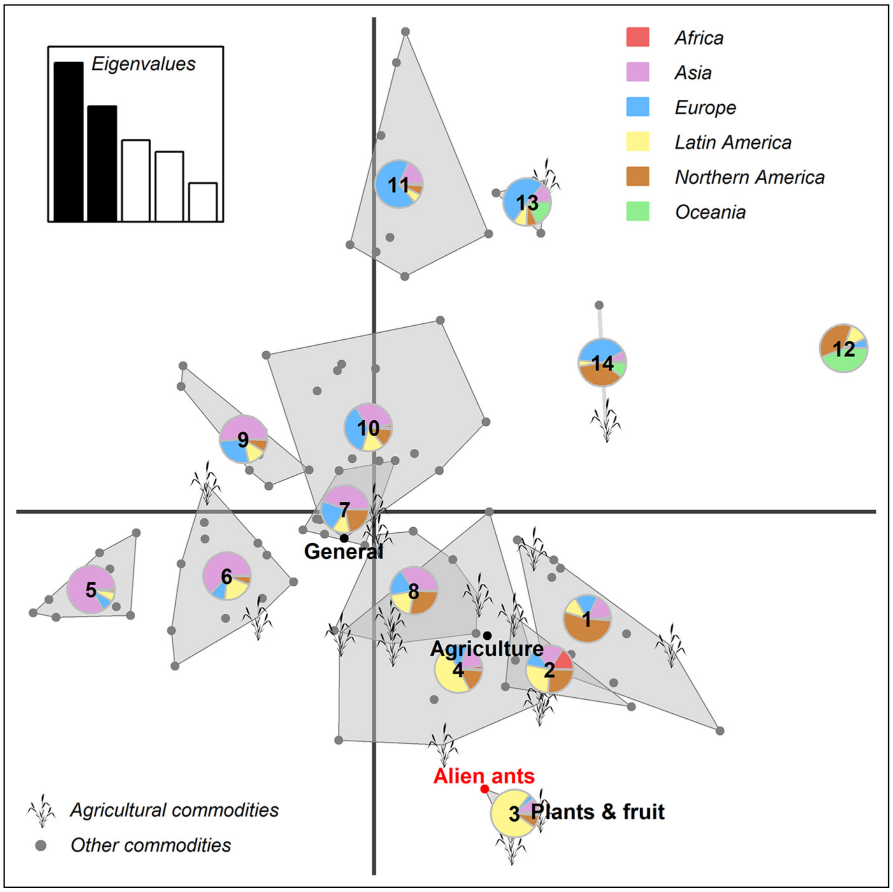

Figure 2. Factorial map of commodity profiles based on their geographic origins. Each solid gray circle represents a commodity category associated with a cluster or group of commodities; in all, there are 14 clusters/groups of commodities with shared similar import profiles of geographic origins. At the center of each commodity cluster is a pie chart representing the average import profile per cluster. General trade, agricultural trade, plant and fruit trade, and alien ant flows are projected as supplementary individuals. Agricultural commodities are found in 10 of the 14 clusters and are denoted by wheat plant icons.

of commodities that shared similar import profiles of geographic origins (Figures 2 and 3).

This analysis revealed that the flows of alien ants and the plant and fruit trade are part of the same group of import profiles, and are strongly linked to Latin America (Figure 3, group 3). The only individual commodity categories that were also in this cluster were 07 (vegetables and fruits) and 08 (cut flowers and ornamental foliage), both of which are part of the plant and fruit trade. All of the other 95 individual commodity flows differed significantly from alien ant flows. The flows of general imports and agricultural imports were both clustered in distant groups (Figure 3).

Although agricultural trade is considered more homogenous than general trade, we found that the individual commodity categories (01–20) constituting the agricultural trade were spread across 10 of the 14 clusters. This scattering pattern suggests that "agricultural trade" is a mixed bag of extremely variable import profiles (Figure 2) and is unlikely to predict the spread of an agricultural pest that is strongly associated with a particular agricultural commodity.

Conclusions

General metrics may sometimes be useful proxies of species transport and have been associated with invasion patterns at large spatial scales (Kalusová *et al*. 2017; Turbelin *et al*. 2017). However, trade as a driver of invasions should not be rejected based on general metrics of trade only, as focusing solely on general trade metrics may blur the association between trade flows and invasion flows. Highly disaggregated trade flows are frequently used in the trade literature but not in the literature on invasive species. Specific trade metrics are likely to be more effective than general trade metrics for use in predicting the geographic origins of future invaders in the US because future trade relationships among nations are likely to change and emerging economies are increasingly contributing to global trade (Dalmazzone 2000). Trade networks of different commodity groups may shift to different world regions or increase at different rates. In the US, for example, live plant imports – a major introduction pathway for many insects and pathogens – are increasing at a much faster rate than other imports (Liebhold *et al*. 2012). Ideally, studies forecasting future invasion risks should determine the actual transport vectors of a taxon of interest. Possible sources of information about transport vectors of invasive species include data collected by biosecurity services conducting interceptions at ports of entry. Unfortunately, such data are only collected by a handful of countries and are subject to biases associated with the methods used to surveil incoming commodities, which can vary in space and over time (Bacon *et al*. 2012). In the absence of detailed information about the commodities transporting a taxon of interest, conducting an exploratory CA based on all possible commodity categories is worthwhile but cannot replace information about the species' biology and propensity to be associated with certain commodities.

It is also important to acknowledge that "more precise" trade data do not necessarily lead to better predictions, as generality will trade off with specificity at some point. Here, we analyzed data for ant flows – but within ants, there may be species-specific commodity associations. For instance, certain ant species may be more associated with certain commodities as compared with other ant species. To make predictions for ants generally, the fruit and plant trade would appear to be an appropriate level of precision, whereas more precise commodity categories (eg the pineapple trade, the orchid trade, and so on) may be more effective for generating predictions of species strongly associated with these particular commodities. A challenge for scientists and biosecurity inspectors is to explore the degree of commodity specificity more broadly across invasive insects. It is crucial for understanding and predicting invasions to examine whether most invasive species travel on a variety of commodities, a restricted set of agricultural commodities (eg plants and fruits), or a specific type of commodity (eg orchids), and for which taxonomic levels we can generalize (ie if there are common commodity profiles for some orders or families).

The relevance of our findings is likely to vary among countries. In the US, the geographic origins of plant and fruit imports differed markedly from origins of general imports. However, in other countries, numerous commodities are imported from the same geographic region. Therefore, for those other countries, the geographic origins of plant and fruit imports will be similar to the geographic origins of other commodities.

Knowledge about commodity associations of invasive species is critical for developing better surveillance policies and improving risk assessments. Countries can be important trading partners, yet not constitute a major biosecurity risk if they do not exchange the relevant commodities. There are longstanding international policies, such as the International Plant Protection Convention standards, linked to the World Trade Organization's Agreement on Sanitary and Phytosanitary Measures. These agreements require that risk assessments be conducted before restrictive measures are implemented for particular species or commodities (Baker *et al*. 2005). Such risk assessments must comply with accepted scientific standards of data acquisition and analysis. This burden of proof is relatively onerous because most modern-day multilateral trade agreements place constraints on the use of nontariff measures, including phytosanitary regulations (Ferrier 2014). It has been argued that some countries use these measures to protect domestic producers. Because phytosanitary regulations can be enacted only if they are justified by risk analysis (Baker *et al*. 2005), bans, post-entry treatments, or quarantine measures are implemented only for a handful of species and associated commodities. These species are typically economically important pests that pose a threat to agricultural interests, human livelihoods, and human/animal health. For instance, the US Department of Agriculture Animal and Plant Health Inspection Service has implemented policies for preventing the spread of only two species of fire ants via the commodity trade. Therefore, gaining a broader understanding of the specific types of trade that transport ants – particularly species with little or no economic impact – is crucial. More than 240 species of ants have established invasive populations somewhere in the world (Bertelsmeier 2021), but most of these species have not been studied enough to know whether they cause any impacts, and many species have impacts on native biodiversity but do not necessarily cause economic losses (Holway *et al*. 2002).

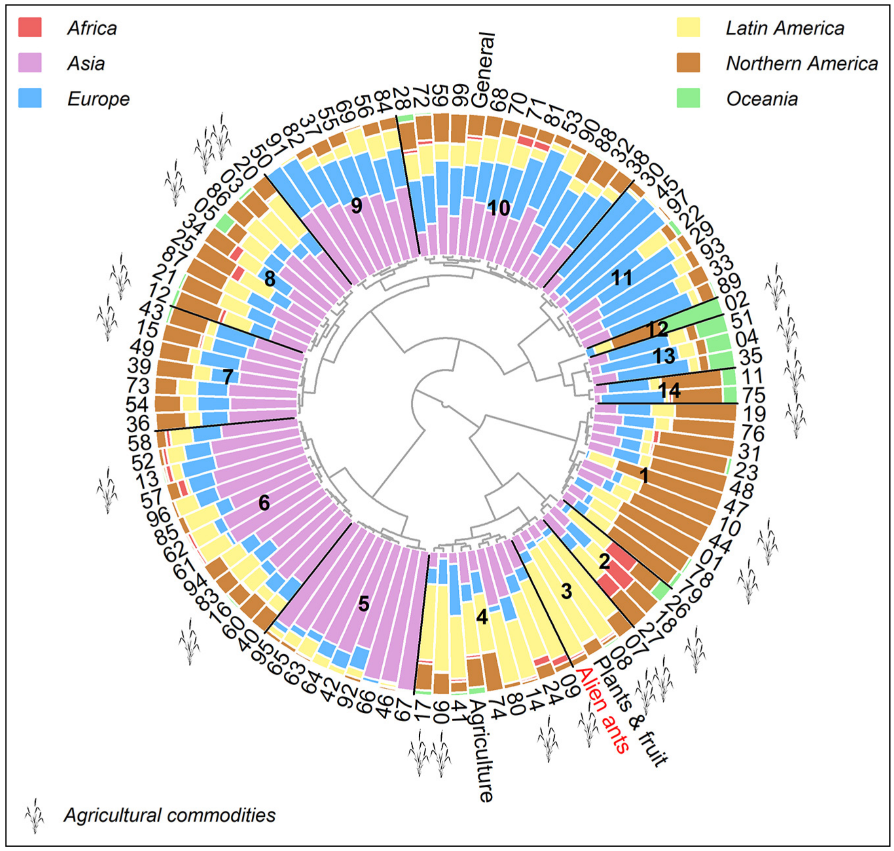

Figure 3. Hierarchical classification of the import profiles of 97 commodity categories and general trade, agricultural trade, plant and fruit trade, and alien ant flows. The barplots represent the geographic origins of these flows. Commodity group numbers (1–14) are indicated at the center of the barplots, and the commodity category code is indicated at the extremity of each barplot. Group 1 is dominated by imports from Northern America; group 2 is characterized by a relatively strong participation of Africa; groups 3 and 4 are dominated by imports from Latin America; groups 5, 6, 7, and 9 by imports from Asia; group 11 by imports from Europe; group 12 by imports from Oceania; and the remaining groups (8, 10, and 14) have a more balanced mix of origins. See WebTable 2 for commodity codes.

In addition to the banning and regulation of specific species, there are also phytosanitary regulations for the importation of fruits and plants in the US, in which these commodities are subjected to inspection and disinfection at the port of first arrival. If an inspector finds species that are considered "plant pests" on fruits or vegetables, the owner or agent of the owner is required to clean or treat the infested goods following the decision by the inspector (CFR 2019). The list of species considered "plant pests" but not covered by any species-specific bans is much longer and encompasses entire groups of species, including all members of the Formicidae family (ants; USDA 2020). Therefore, if an inspector finds ants on inspected commodities, those commodities will be subjected to treatment. In many countries, biosecurity services constantly monitor and adjust inspections based on risk-based sampling and other data-driven targeting (B Caton pers comm). However, because countries retain the right to decide what constitutes acceptable risk, the list of recorded and regulated species varies enormously from country to country (Eschen *et al*. 2015). Nonetheless, global biosecurity inspections provide a window into the ongoing transport of insects worldwide (Turner *et al*. 2021) and data on commodity associations of specific taxonomic groups obtained through biosecurity interceptions could inform predictions of potential future species flows.

A better understanding of these global species flows could also improve current prevention practices. The most effective approach to invasive ant management globally is believed to be active prevention, not at the location of entry of a country but at the port-of-exit to avert contamination elsewhere (Hoffmann *et al*. 2010). In this respect, New Zealand has the most proactive policy through extension of its biosecurity activities to ports in three nearby nations. Pretreatment of goods prior to arrival in New Zealand has led to a 98.5% reduction in contamination rates of arriving commodities within a year, and represents an extremely cost-efficient approach (Hoffmann *et al*. 2010). Although New Zealand imports many goods from a few Pacific Island nations that are financially dependent on the country, a general policy of biosecurity actions at the port-of-exit is likely unfeasible for most nations. Therefore, identifying precisely which commodities pose the greatest risk and identifying the geographic origins of those commodities may help target specific countries where implementation of similar policies might be viable.

Information about species flows could also be used to improve risk assessments, which are crucial for allocating resources for prevention and surveillance within a focal country (Epanchin-Niell and Liebhold 2015). Combining knowledge – of the specific commodities likely to transport the ant species of interest (based on biosecurity interception data), of the current distribution of the ant species, and of the global trade network of flows of these commodities – will enhance assessments of introduction risk. Once a species is considered a high risk for a focal country, surveillance programs can be established. For example, theoretical models of optimal detection of ant incursions (Ujiyama and Tsuji 2018; Bradhurst *et al*. 2021) can be developed to inform optimal surveillance efforts by humans or "sniffer" dogs (Poland and Rassati 2019). Approximately half of the more than 300 recorded ant eradication programs worldwide have been successful, and their probability of success was highest when the infested area was still small (<10 ha; Hoffmann *et al*. 2016), underscoring the need for accurate predictions of introduction risks based on global flows of species.

Our analyses provide a quantitative comparison of 97 commodity flows from six world regions to the US, and demonstrate that only the plant and fruit trade (and two commodity categories that are part of this trade: namely, "vegetables and fruits" along with "cut flowers and ornamental foliage") was strongly associated with the geographic origins of alien ant flows. These findings have important implications for improving our understanding of intercontinental species exchanges, as more precise knowledge of the commodity trade is necessary for identifying links between invasion flows and the movement of goods.

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Data Availability Statement

All data and the R code used in our analyses are available on Dryad (doi.org/10.5061/dryad.w0vt4b8nz). The analyses were carried out in R (v4.0.3). We used the *tradestatistics* package (Vargas 2020) to access UN open trade data.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2509/suppinfo