

Surveys and Needs Assessments

Recent Immigrant Insect Fauna—Another Look at a Classic Analysis

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Abstract

In 1978, Reece Sailer published a seminal retrospective entitled ‘Our Immigrant Insect Fauna.’ His goals were to better understand the origins and historical patterns of alien insect species introductions into the United States and establish a baseline for future work to improve our ability to respond to environmental and agricultural well-being threats. We updated Sailer’s study to include information on species introduced recently into the United States and that are now targeted by regulatory agencies. The recent trends (recorded through 2016) are different from those reported by Sailer. Asian-origin species are much more important than in 1978 and predominate today. Nevertheless, introductions from all parts of the world have continued. Although the diversity of alien species’ origins has increased through time, there has not been a corresponding change in the rate of introductions of species of phytosanitary importance. This finding is inconsistent with our original assumption of a positive nonlinear relationship with international trade imports. Our findings will assist in identifying and prioritizing potential high-risk plant pests as well as enhancing biosecurity capacities.

Key words: invasive species, phytosanitary, immigrant fauna, invasive trend, trade

Invasive alien species are known to cause significant economic and environmental impacts. In one of the first studies of its kind, [Pimentel et al. \(2005\)](#) estimated the total economic costs of invasive alien species in the United States to be ≈US\$120 billion per year. More recent studies by [Bradshaw et al. \(2016\)](#) and [Diagne et al. \(2021\)](#) estimated that invasive insect species cost at least US\$77 billion and US\$83.3 billion globally per year, respectively. Since these studies are based on conservative assumptions and incomplete information, their estimates of the economic losses caused by invasive alien species are presumed to be gross underestimates ([Aukema et al. 2011](#), [Nghiem et al. 2013](#), [Diagne et al. 2021](#)). For example, data on the human health costs of invasive species are not always available. In the United States, the budgets of federal agencies like the U.S. Department of Agriculture (USDA) and the U.S. Geological Survey (USGS)—both of which have invasive alien species as a priority issue—are upwards of US\$1 billion per year ([USDA 2015](#)). In addition, economic analyses for known plant pests like fruit flies (Diptera: Tephritidae spp.), the Asian longhorned beetle (*Anoplophora glabripennis* Motshulsky

(Coleoptera: Cerambycidae)), and the emerald ash borer (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)) have projected impacts in the billions of U.S. dollars ([Nowak et al. 2001](#), [Kovacs et al. 2010](#)). Furthermore, their ecological effects can extend well beyond the obvious economic damage from host losses and mitigation costs ([Kenis et al. 2009](#)). For instance, insects such as the emerald ash borer and the hemlock woolly adelgid (*Adelges tsugae* Annand (Hemiptera: Adelgidae)) have altered U.S. forested ecosystems permanently in the decades since their arrival ([Orwig and Foster 1998](#), [Herms and McCullough 2014](#)).

Alien species, particularly alien plant pests, are often introduced unintentionally because of trade linked to globalization ([Levine and D’Antonio 2003](#), [Hulme 2009](#), [Aukema et al. 2010](#), [Koch et al. 2011](#), [Nghiem et al. 2013](#), [Paini et al. 2016](#)). Since 1970, the volume of global commodity imports has increased four-fold ([Hulme 2009](#)) and is expected to continue to increase. However, the degree of growth is uncertain due to numerous factors, such as economic policy uncertainty ([Constantinescu et al. 2017](#)). In

turn, this uncertainty makes it challenging to forecast the entry and establishment of alien species in the United States (or elsewhere) based on trade.

Each year, many species arrive in the United States (McCullough et al. 2006). However, only a small fraction of those presumably novel species become established, and a smaller number become economically or environmentally detrimental (Williamson and Fitter 1996, Liebhold and Tobin 2008, Aukema et al. 2010). Critical factors for successful establishment after entry include finding suitable host species and environmental conditions and arriving in sufficient numbers to overcome genetic bottlenecks, Allee effects, and abiotic limitations.

As global trade and human travel increase each year, the likelihood of introducing new invasive species increases (Levine and D'Antonio 2003, Hulme 2009, Aukema et al. 2010, Koch et al. 2011, Nghiem et al. 2013, Paini et al. 2016). Thus, identifying types of species that could be introduced, potential establishment rates, and areas most at risk due to the expansion of global trade could help identify imminent threats and prevent further introductions of devastating alien species into the United States. Several studies have examined historical patterns of alien species introductions (Sailer 1978, Mack 2003, Aukema et al. 2010). Sailer (1978) is of particular interest to this study because he provided a baseline for the United States for trends and patterns associated with introduced arthropod species. His study centered on immigrant Insecta and Acari species and examined trends by taxonomy, origin (native range), and economic importance. His study indicated that the introduction of such species into the continental United States was closely related to historical trade patterns; the numbers of species introduced each year corresponded with foreign trade levels, and most alien species originated from Europe (Sailer 1978). Similar studies have been conducted for wood-boring forest insects (Koch et al. 2011), forest insect and pathogen species (Aukema et al. 2010), and plants (Mack 2003) introduced to the United States. In addition, a few studies examined alien species in other parts of the world (Kiritani 1998, Roques 2010, Seebens et al. 2017, Seebens et al. 2021). These studies suggested that the primary origin of alien species—particularly those associated with forests—was likely to shift from Europe to Asia due to increased trade with Asian countries (Aukema et al. 2010, Koch et al. 2011).

In this study, we characterize unintentional introduction patterns since 1980 and contrast them with the baseline created by Sailer (1978). The trend analysis is intended to help plan for large-area management to minimize new introductions to the United States and identify a needed framework to predict the location-specific likelihood of introductions.

Trade and Passenger Data Collection

Trade and air passenger data were obtained to understand recent trend changes and to find correlations between recognized plant pest pathways and alien species introductions in recent years. Annual numbers of people who traveled to a country other than that of their residence for a period not exceeding 12 mo were collected since 1995 using the World Development Indicators database of the World Bank (<https://databank.worldbank.org/source/world-development-indicators>). Annual U.S. inbound passenger numbers since 1995 were summarized using the T-100 International Market database of the U.S. Department of Transportation, Bureau of Transportation Statistics (<https://www.bts.gov/topics/passenger-travel>).

Global and U.S. trade data since 1980 were obtained from an international trade statistics database administered by the World

Trade Organization (<https://data.wto.org/>) and a historical series database administered by the U.S. Census Bureau (<https://www.census.gov/foreign-trade/statistics/historical/index.html>). U.S. agricultural commodity import and export trade values were obtained using the Global Agricultural Trade System developed by the USDA Foreign Agricultural Service (<https://apps.fas.usda.gov/GATS/default.aspx>). We summarized the agricultural commodity import and export values by region.

Invasive Alien Species Data Collection

Information about alien species that have entered and become successfully established in the United States was gathered from the North American Non-Indigenous Arthropod Database (NANIAD) and the New Pest Advisory Group (NPAG) Database. The NANIAD was developed in the early 1990s by K.C. Kim at Pennsylvania State University in cooperation with USDA APHIS Plant Protection and Quarantine (PPQ). The NANIAD includes approximately 2,400 nonindigenous insect species established since 1565. Although the latest record added to this database was in 1991, most species were established in the United States before 1983. Notably, the NANIAD includes many arthropods intentionally introduced to the United States as beneficial species or biological control agents. The NPAG Database is updated and maintained by USDA APHIS PPQ. The NPAG team assesses alien plant pests that are new or imminent threats to U.S. agriculture or the environment and recommends appropriate actions to PPQ. Currently, the database contains over 1,000 species of arthropods, plant pathogens, weed, and mollusks recorded since 1980 (as of December 2016). Because imminent and intercepted (e.g., via border inspection) species were not considered as successfully established species, they were not included in this study. Moreover, the NPAG Database, unlike the NANIAD, does not include species that have been deliberately introduced to the United States (e.g., as biological control agents). In our analysis, we focused on unintentionally introduced Insecta and Acari species recognized as plant pests because the objectives of this study were to understand the historical trends of accidental plant pest introductions to the United States and use these findings to improve plant biosecurity. Therefore, we excluded plant pathogen, weed, and mollusk records from the NPAG Database for this study.

Missing data were compiled using literature search and input from subject matter experts in USDA APHIS PPQ. Species with unavailable data elements (i.e., origin and/or location where first introduced) after this compilation process were included in the total number of newly introduced alien species since 1980 but were excluded from the analysis on introduced locations or the analysis on pest origin depending on the type of missing data. There were 20 records that were only identified to genus level.

Evaluation of Historical Alien Species Introductions in the United States

Unintentionally introduced alien insect (Arthropoda: Insecta) and mite (Arthropoda: Arachnida: Acari) species in the United States since 1980 were evaluated by combining and analyzing the NANIAD and the NPAG Database. We first determined if the number of alien insect and mite species established per year increased as air travelers and trade had increased. Then, we evaluated the pattern of alien species accumulation using a regression model to determine whether the annual number of established alien species increased in a positive nonlinear fashion or remained constant.

Some taxonomic classifications have changed since 1978. For example, Sailer (1978) summarized the alien insect and mite species in eight

major orders (Homoptera, Hymenoptera, Coleoptera, Lepidoptera, Acarina, Thysanoptera, Diptera, and Heteroptera) and ten minor orders (Orthoptera, Psocoptera, Thysanura, Dermaptera, Neuroptera, Anoplura, Araneida, Embioptera, Isoptera, and Siphonaptera). Currently, Homoptera and Heteroptera are suborders under Hemiptera. Consequently, we merged these two suborders into Hemiptera and grouped the number of alien species established in the United States into seven major orders (Hemiptera, Coleoptera, Lepidoptera, Diptera, Thysanoptera, Hymenoptera, and Acari) as well as an 'other' category.

Both databases contain data fields for documenting the date of the first U.S. detection, the first detection location (typically reported at the state level), and the native region of the species. However, many records in each database lacked this information. In such cases, we estimated the origin of a given species through extensive literature search and the first detection date and location based on the first public record or the oldest literature citation that recorded a species' presence in the United States.

Trends in new pest establishments were assessed by evaluating the pest origins and the locations where the pests were first detected in the United States. We used continental-scale regions that enabled comparison between Sailer (1978) and our analysis. Some species had wide native ranges and were identified as native to two or three regions (e.g., Eastern Palearctic and Oriental regions, Eastern and Western Palearctic regions). For those species reported to be native to more than one zoogeographic region, their native ranges were described by combining the regions. In turn, the origins of the alien arthropod species established in the United States were categorized into eight continental-scale regions: 1) North America (Nearctic), 2) Central and South America (Neotropical), 3) Europe (Western Palearctic), 4) Asia (Eastern Palearctic and Oriental), 5) Africa (Ethiopian), 6) Oceania (Australian and Oceania), 7) Asia-Australian, and 8) unknown (Fig. 1). For species identified as originating from both the Eastern and Western Palearctic regions, half were assigned to Western Palearctic (Europe) and the other half were assigned to Eastern Palearctic (Asia) to avoid double-counting. In addition, the first detected locations of the alien species since 1980 were summarized at the state level to determine whether some states were more susceptible to other states.

Results

Plant Pest Pathways and Recent Changes

Approximately 1.025 billion people traveled outside of their usual country of residence in 1995, while there were more than 2.032

billion world travelers in 2016 (World Bank 2021) (Fig. 2). Thus, the number of world travelers doubled in 20 yr. Similarly, the U.S. inbound (arrivals) passengers increased more than two-fold from 1995 to 2016, with 52 million and 107 million inbound passengers to the United States in 1995 and 2016, respectively (USDOT 2021) (Fig. 2). The world traveler and U.S. inbound traveler patterns were also very similar through time. There was a constant increase from 1995 to 2000, followed by a decrease in travelers from 2000 to 2003. Since 2009, there has been a constant linear increase for world travelers and U.S. inbound passengers.

Global trade has increased almost nine-fold since 1980 (WTO 2021) (Fig. 3). The U.S. import and export trends increased similarly (Fig. 3). For example, in the early 1980s, the U.S. import and export trade values were about the same (US\$230 billion); however, in 2016, imported and exported goods were valued at US\$2.2 trillion and US\$1.5 trillion, respectively.

Trade of agricultural commodities in the United States has also increased significantly since 1980 (Fig. 4). The trajectories for U.S. agricultural commodity export and import values through time were similar, although export values were always more than import values (USDA-FAS 2021). The U.S. agricultural commodity import value in 2016 was more than six times the value in 1980. South America and Europe were the leading partners for agricultural commodity imports to the United States in the early 1980s (Table 1). As of 2016, the leading partners for U.S. agricultural commodity imports were Canada and Mexico (North America), and agricultural commodity import values from these two countries increased more than 2,000% since 1980. The value of imports from Europe and Asia increased more than 800% since 1980, while the value of imports from all regions increased more than 600%.

There was also a noticeable change in the pattern of trade in fresh fruits and vegetables (Fig. 4). The values of U.S. imports and exports of fresh fruits and vegetables were similar in the early 1980s. Over time, fruit and vegetable imports to the United States increased more than U.S. exports. In 2016, the United States imported more than US\$20 billion of fresh fruits and vegetables while exporting approximately US\$7 billion. The fresh fruit and vegetable import values were summarized by regions (Table 2). Fresh commodity imports to the United States increased significantly from all regions. Fresh commodity imports from Europe and Asia increased 30-fold and 45-fold since 1980, respectively, but the most pronounced change was in imports from the Middle East ($\approx 14,000\%$) since 1980. However, the



Fig. 1. Geographic regions used for categorization of species origin.

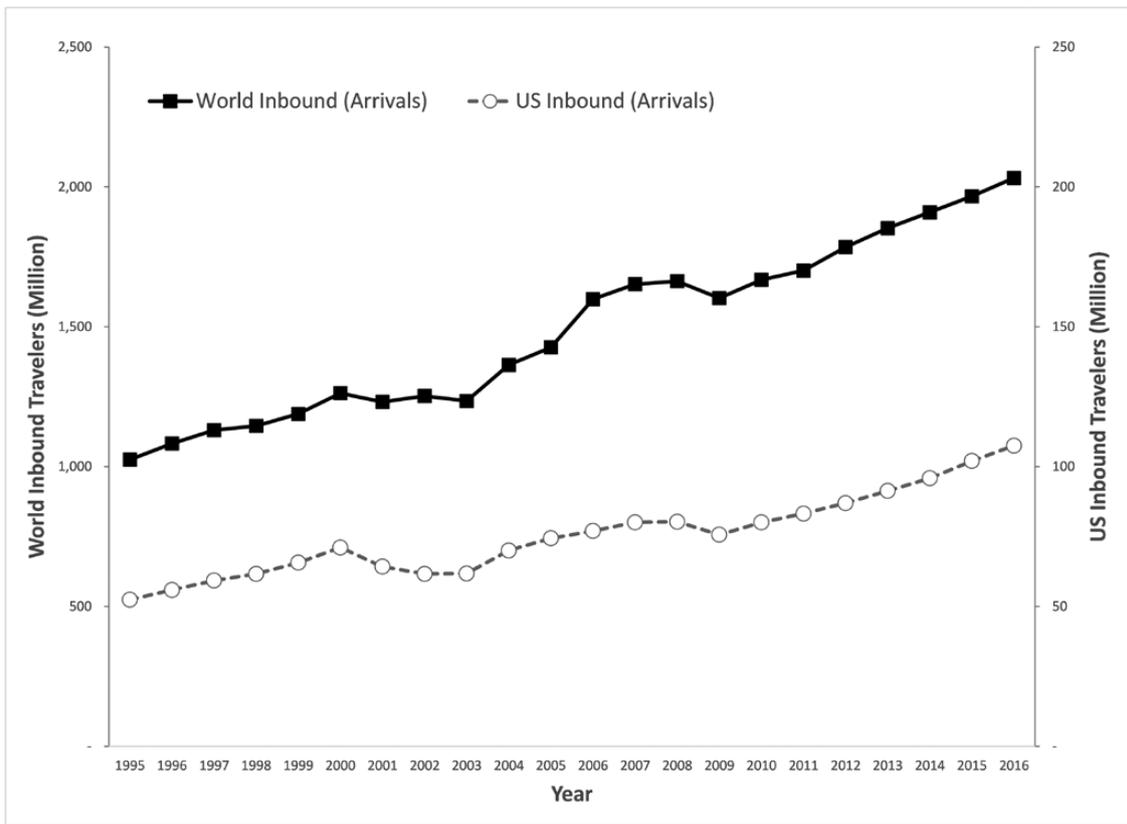


Fig. 2. Annual number of world air traffic passengers and U.S. inbound air passengers since 1995.

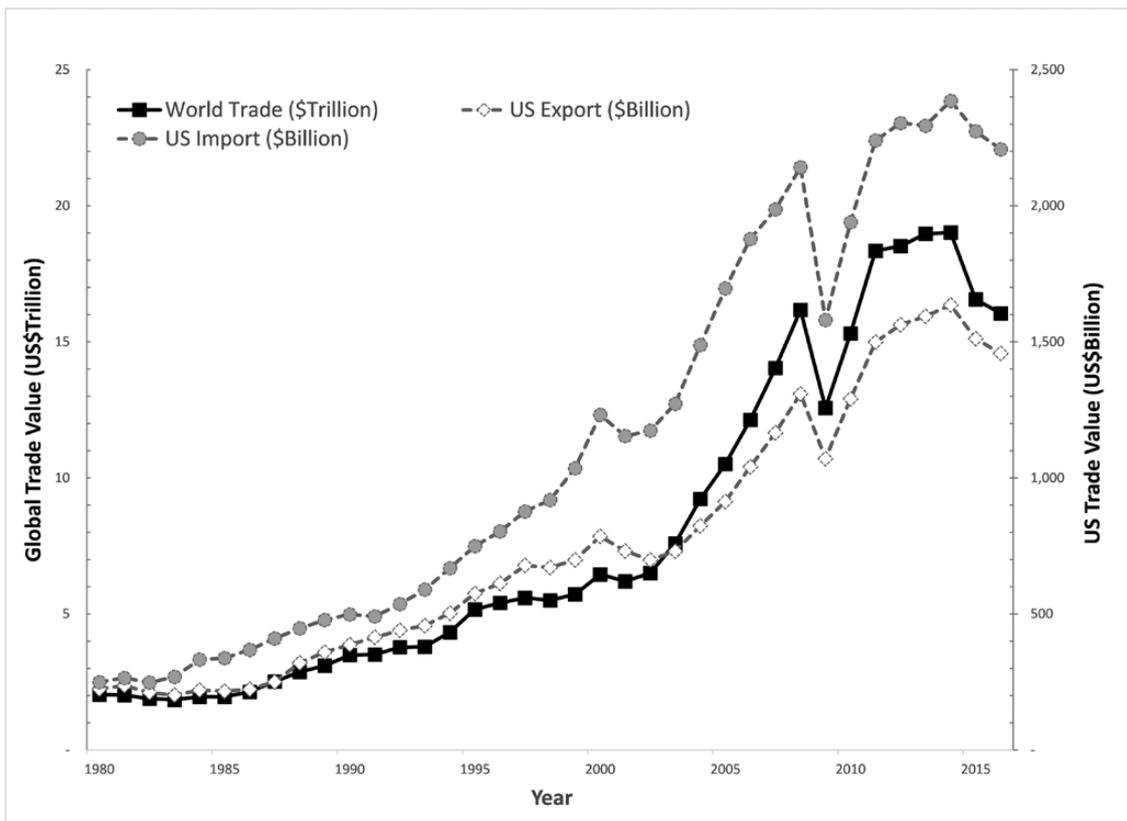


Fig. 3. Global trade and U.S. import and export values from 1980 to 2016.

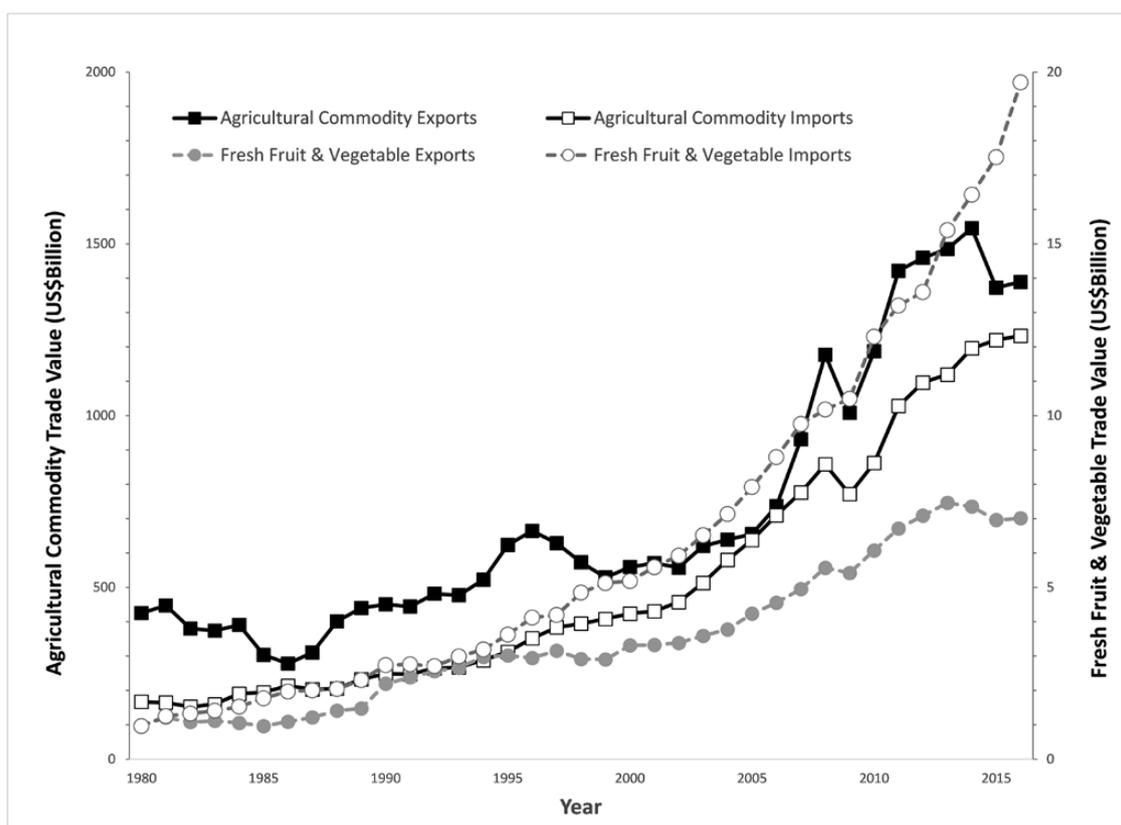


Fig. 4. U.S. agricultural commodity import and export values and U.S. fresh fruit/vegetable import and export values.

Table 1. U.S. annual average agricultural commodity import values and percent change from 1980 to 2016 by regions (US\$ million) (USDA-FAS 2021)

Regions	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2016	% change
North America	2,605	4,367	7,527	12,213	17,090	25,943	38,176	45,647	2,056
Central America	1,899	1,834	1,951	2,747	2,816	4,411	6,067	6,622	208
South America	3,642	4,109	3,921	5,010	5,224	9,181	13,518	14,257	248
Europe	3,481	5,244	6,909	9,283	12,886	19,321	23,228	27,894	847
Asia	2,030	2,459	2,931	4,387	5,132	9,574	16,528	17,247	810
Middle East	298	352	475	600	570	785	1,031	1,424	688
Oceania	1,562	1,729	1,982	1,933	3,370	4,354	5,156	6,694	222
Africa	1,184	889	632	841	1,005	1,513	2,332	2,837	108
Total	16,701	20,983	26,328	37,014	48,093	75,082	106,037	122,622	638

Table 2. U.S. annual average fresh fruit and vegetable import values and percent change from 1980 to 2016 by regions (US\$ million) (USDA-FAS 2021)

Regions	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2016	% change
North America	562	769	1,226	2,119	3,081	5,207	8,441	11,450	2,715
Central America	392	545	662	914	1,097	1,525	2,279	2,672	781
South America	280	570	800	991	1,398	2,123	2,801	3,605	2,104
Europe	16	49	74	192	236	205	193	238	3,053
Asia	9	23	33	37	73	166	255	320	4,524
Middle East	3	5	4	14	35	17	18	42	14,028
Oceania	23	51	63	90	103	110	98	141	791
Africa	10	6	13	27	44	70	97	141	1,411
Total	1,295	2,017	2,875	4,383	6,068	9,425	14,183	18,608	1,948

amounts of fresh commodity imports from the Middle East were minimal compared to other regions.

Alien Arthropod Introductions in the United States

The number of alien insect and mite species that entered unintentionally and established in the United States since 1980 was 388. Those species belonged to 320 genera, 111 families, and 13 orders (i.e., 12 insect orders and one subclass, Acari, within class Arachnida). All records were included to estimate annual introduction rates, but records only identified to genus level were removed from further analyses. Although the number of recorded alien species varied from year to year, there was a consistent and nearly constant (i.e., linear) increasing trend in cumulative alien species introductions since 1980

($y = 11.2x + 13.12$; $R^2 = 0.996$; $F_{1,35} = 7892$, $P < 0.001$) (Fig. 5). On average, 11.2 new insect or mite species (standard deviation = 4.6) were recorded as having entered and established in the United States successfully each year since 1980.

Analysis of Trends Associated with Alien Arthropods

Most alien insect and mite species discovered in the United States after 1980 belong to the order Hemiptera, followed by Coleoptera and Lepidoptera (Table 3). The proportional representation of Hymenoptera species decreased substantially in comparison to the proportion before 1978. Sailer (1978) reported that Hymenoptera accounted for 19.6% of all immigrant insect and mite species in the United States, while the order represented only 6.9% of all insect

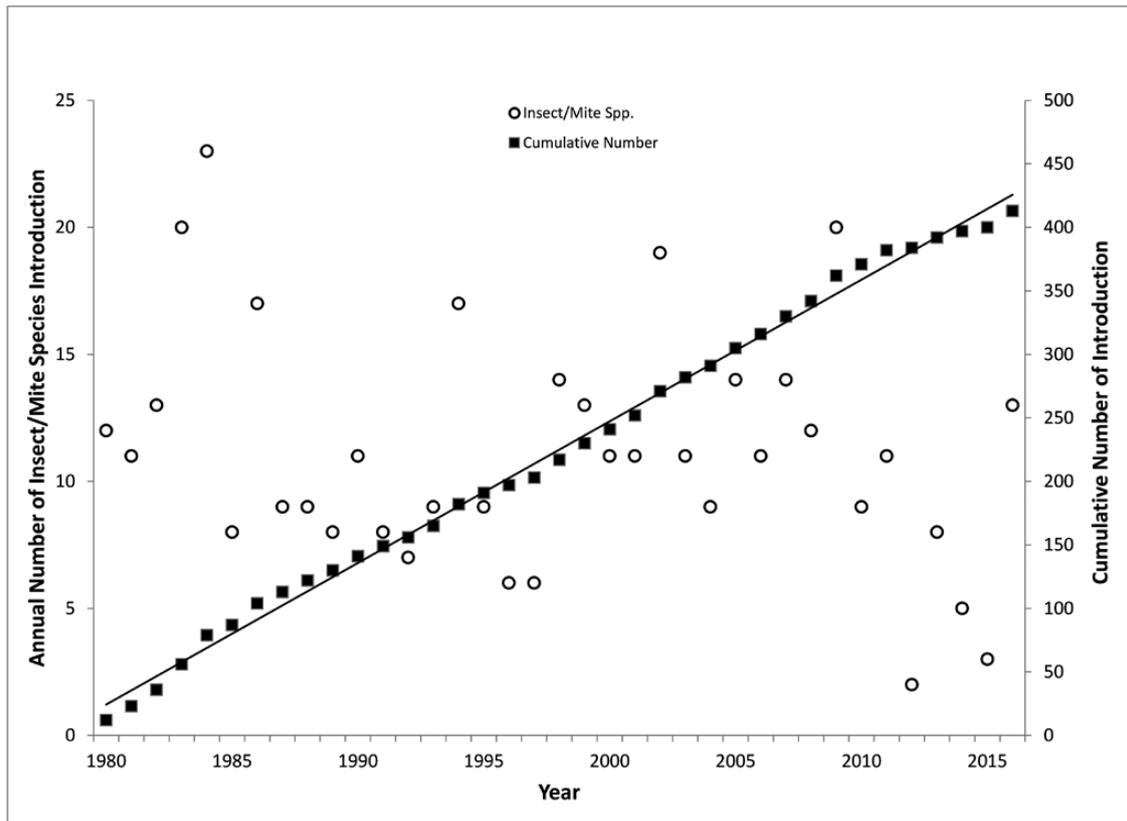


Fig. 5. Number of insect/mite species unintentionally introduced and established to the United States since 1980 (Sources: NANIAD and NPAG).

Table 3. Taxonomy of plant pests (insects and mites) that were introduced to the United States from 1980 to 2016 based on NANIAD and NPAG Database

Order or Subclass	1980-1989	1990-1999	2000-2009	2010-2016	Total	Proportion since 1980 (%)	Before 1978	Proportion before 1978 (%)
Hemiptera	38	29	44	18	129	33.3	382	27.6
Coleoptera	28	22	34	13	97	25.0	295	21.3
Lepidoptera	9	12	10	8	39	10.1	120	8.7
Diptera	16	10	8	3	37	9.5	86	6.2
Thysanoptera	6	11	9	2	28	7.2	80	5.8
Hymenoptera	14	3	7	3	27	6.9	272	19.6
Acari	8	4	9	3	24	6.2	79	5.7
Others	4	1	2	0	7	1.8	71	5.1
Total	123	92	123	50	388	100	1385	100

The introduction data before 1978 were obtained from Sailer (1978). Others include Orthoptera, Psocoptera, Thysanura, Dermaptera, Neuroptera, Anoplura, Araneida, Embioptera, Isoptera, and Siphonaptera. The proportions of species by order/subclass before 1978 and after 1980 are reported as percentages.

greatest number of alien species first detections since 1980. The state is a well-known hub for trade and human movement, especially from Caribbean, Central American, and South American countries (Caton et al. 2006). California and Hawaii ranked second and third, respectively. Both states have high international trade and human movement volumes, mainly from Asia and the Pacific Islands. Other significant states were Washington, Oregon, New York, and Texas, which border Canada or Mexico. In contrast, the central United States had no first detections of alien insect or mite species.

Discussion

Using the NANIAD and the NPAG Database, we analyzed nonindigenous arthropod plant pests accidentally introduced into the United States to determine the annual number of species introduced since 1980, as well as their taxonomic groups, regions of origin, and entry locations. Understanding recent trends would enhance safeguarding protocols, and this study highlighted the recent alien species introduction patterns compared to the ones before 1978. As Sailer (1978) and others (Hulme 2009, Aukema et al. 2010, Koch et al. 2011, Nghiem et al. 2013) predicted, new insect and mite species were introduced every year since 1980. The most noteworthy change with respect to recent (i.e., after 1980) alien species introductions compared with those before 1978 was a shift in the most common regions of origin (geographic source). We observed a trend in the origin being increasingly from Asian countries and away from Europe as foreign trade patterns continue to emphasize trade with Asia.

The proportions of species in the Hemiptera, Coleoptera, and Diptera orders increased considerably since 1980 compared to the species introduced before 1978. Hemiptera and Diptera species are easily transported with nursery stock, propagative materials, and fresh fruits and vegetables (Liquido et al. 1995, Areal et al. 2008). Coleoptera species introductions may be explained by expanded usage of solid wood packing materials (SWPM) in the United States and elsewhere during the 1980s and 1990s, driven by the increase in global trade (Lidsky 2003, Haack et al. 2014). As a result of the increased wood-boring insect introductions, ISPM 15 (International Standards for Phytosanitary Measures: ISPM) was developed by the International Plant Protection Convention (IPPC) (IPPC 2018). Records from 2003 to 2009 for U.S. ports of entry suggest that infested wood packing materials were reduced after the United States implemented ISPM 15 in 2005 (Haack et al. 2014).

We hypothesized that the rate of accidental insect and mite species introductions since 1980 would be greater than the rate found by Sailer (1978, 1983) due to a significant increase in global trade and tourism. The annual accidental introduction rate for insects and mites since 1980 was 11.2 species, which was only moderately higher than the rate of 9 species per year reported by Sailer (1978). Sailer (1983) later reexamined alien arthropod establishments and reported approximately 11 accidental species introductions per year from 1920 to 1980, indicating the rate of arthropod establishment in the United States may have been constant since 1920. This result, which contradicts our hypothesis, was consistent with the findings of Aukema et al. (2010) regarding alien forest insect species. Federal agencies are indeed focusing on safeguarding against and preventing species invasions using more efficient monitoring systems and better diagnostic tools (Aukema et al. 2010). As the national plant protection organization (NPPO) for the United States, APHIS PPQ develops and maintains a phytosanitary early-warning system to collect pest information at a global scale that tracks overseas outbreaks and global movement of insects and diseases. It then prioritizes alien

plant pests that are not known to be established in the United States to efficiently allocate resources to manage those key species before they become established.

The number of pests recorded in the NANIAD and the NPAG Database since 1980 seems low. Yamanaka et al. (2015) listed 3540 and 2651 nonindigenous insect species in North America and Hawaii, respectively. Our low number of records, by comparison, may be because 1) APHIS PPQ, as the primary force behind both the NANIAD and the NPAG Database, focuses on species that are identified as quarantine pests according to the IPPC definition (IPPC 2007); 2) some species are only officially reported when they cause visible damage in certain geographic areas; and 3) Yamanaka et al. (2015) listed species alien to North America (i.e., both the United States and Canada), including more than 300 deliberately introduced species, while our study focused on insect and mite species unintentionally introduced in the United States.

Another notable finding was that most alien insect and mite species recorded since 1980 were first established in one of six states: Florida, California, Hawaii, Washington, Oregon, and Texas. The majority of traded commodities, including live plants, enter the United States through airports, seaports, and cities in those states (Colunga-Garcia et al. 2013, Nguyen et al. 2013). In addition, those states tend to have mild winter temperatures and diverse plant species (i.e., potential hosts), so many alien pests may find suitable conditions. The Central United States was not identified as a prominent first detection location, possibly because it is not surveyed as intensively as those six states (CERIS 2021). Regardless, this does not mean that the Central United States poses no risk as an alien species entry location. There are large volumes of commodity and human movement via highways and railways within North America. In the United States, trucking is the most frequently used mode of freight transportation, accounting for 60% of the total freight weight (USDOT 2006). Together, trucks and rails accounted for 77% of all freight transportation and moved approximately 41.6 million tons of freight a day in 2012. The U.S. Department of Transportation forecasted that freight transportation by trucks and rails would increase to 18.6 billion tons (51 million tons per day) by 2045 (USDOT 2016). These massive movements of freight within the United States could create diverse entry opportunities for invasive alien species. For example, *Lymantria dispar asiatica* Vnukovskij (Lepidoptera: Erebiidae), a subspecies of *L. dispar* not known to be established in the United States, was detected in central Oklahoma City in 2013 (ODA 2013). Although this incursion was subsequently eradicated, it was most likely due to the insect being transported on vehicles or by hitchhiking on cargo (or cargo containers) originating from Asian countries.

This assessment provides recent trends in alien species introductions and identifies needed updates in forecasting and prioritizing insect and mite plant pests that are not established in the United States, as trade and tourism are expected to continue to increase in the near future. The most salient characteristic of trade and human movement over the past few hundred years is globalization's constant crossing of political boundaries. New species may no longer be introduced into the United States only from their native ranges, but also from other regions where they have become established, or perhaps from locations (e.g., busy foreign port cities) that would be considered intermediate or transitory destinations. Network analysis to characterize global and domestic human-assisted movement potential is critical to evaluate and understand the likelihood of plant pest introduction, since species may enter the U.S. via various pathways, some of which are poorly known (or maybe unknown). Compounding this challenge is the fact that species will almost certainly find

additional pathways to enter and invade new areas. Historical trend analyses like our study assist in identifying new pathways and potential high-risk plant pests, even if it is at a relatively coarse scale. In addition, understanding potential pest introduction patterns in specific regions will enable better allocation of response resources to minimize unexpected damage to crops and natural ecosystems.

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References Cited

- Areal, F. J., J. Touza, A. MacLeod, K. Dehnen-Schmutz, C. Perrings, M. G. Palmieri, and N. J. Spence. 2008. Integrating drivers influencing the detection of plant pests carried in the international cut flower trade. *J. Environ. Manage.* 89: 300–307.
- Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. *Bioscience* 60: 886–897.
- Aukema, J. E., B. Leung, K. Kovacs, C. Chivers, K. O. Britton, J. Englin, S. J. Frankel, R. G. Haight, T. P. Holmes, A. M. Liebhold, *et al.* 2011. Economic impacts of non-native forest insects in the continental United States. *Plos One* 6: e24587.
- Bradshaw, C. J., B. Leroy, C. Bellard, D. Roiz, C. Albert, A. Fournier, M. Barbet-Massin, J. M. Salles, F. Simard, and F. Courchamp. 2016. Massive yet grossly underestimated global costs of invasive insects. *Nat. Commun.* 7: 12986.
- Caton, B. P., T. T. Dobbs, and C. F. Brodel. 2006. Arrivals of hitchhiking insect pests on International Cargo Aircraft at Miami International Airport. *Biol. Invasions* 8: 765–785.
- CERIS. 2021. PEST TRACKER, Survey Maps. <https://pest.ceris.purdue.edu/pests.php>. Accessed 31 August 2021.
- Colunga-Garcia, M., R. Haack, R. Magarey, and D. Borchert. 2013. Understanding trade pathways to target biosecurity surveillance. *NeoBiota* 18: 103–118.
- Constantinescu, C., A. Mattoo, and M. Ruta. 2017. Trade developments in 2016: policy uncertainty weights on world trade. World Bank, Washington, D.C.
- Diagne, C., B. Leroy, A. C. Vaissière, R. E. Gozlan, D. Roiz, I. Jarić, J. M. Salles, C. J. A. Bradshaw, and F. Courchamp. 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592: 571–576.
- Haack, R. A., K. O. Britton, E. G. Brockerhoff, J. F. Cavey, L. J. Garrett, M. Kimberley, F. Lowenstein, A. Nuding, L. J. Olson, J. Turner, *et al.* 2014. Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. *Plos One* 9: e96611.
- Herms, D. A., and D. G. McCullough. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annu. Rev. Entomol.* 59: 13–30.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* 46: 10–18.
- IPPC. 2007. ISPM No. 5. Glossary of Phytosanitary Terms, International Standards for Phytosanitary Measures. International Plant Protection Convention, Food and Agriculture Organization of the United Nations, Rome, Italy.
- IPPC. 2018. ISPM No. 15: Regulation of wood packing material in international trade. International Plant Protection Convention, Food and Agriculture Organization of the United Nations, Rome, Italy.
- Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M. J. W. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. *Biol. Invasions* 11: 21–45.
- Kiritani, K. 1998. Exotic insects in Japan. *Entomol. Sci.* 1: 291–298.
- Koch, F. H., D. Yemshanov, M. Colunga-Garcia, R. D. Magarey, and W. D. Smith. 2011. Potential establishment of alien-invasive forest insect species in the United States: where and how many? *Biol. Invasions* 13: 969–985.
- Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecol. Econ.* 69: 569–578.
- Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. *Conserv. Biol.* 17: 322–326.
- Lidsky, M. 2003. Importation of solid wood packing material: Final environmental impact statement—August 2003. United States Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, Riverdale, MD.
- Liebhold, A. M., and P. C. Tobin. 2008. Population ecology of insect invasions and their management. *Annu. Rev. Entomol.* 53: 387–408.
- Liquido, N. J., H. T. Chan, Jr, and G. T. McQuate. 1995. Hawaiian tephritid fruit flies (Diptera): integrity of the infestation-free quarantine procedure for 'Sharwil' avocado. *J. Econ. Entomol.* 88: 85–96.
- Mack, R. N. 2003. Plant naturalizations and invasions in the eastern United States: 1634–1860. *Ann. Mo. Bot. Gard.* 90: 77–90.
- McCullough, D. G., T. T. Work, J. F. Cavey, A. M. Liebhold, and D. Marshall. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. *Biol. Invasions* 8: 611.
- Narendran, T. C. 2001. Parasitic Hymenoptera and biological control, pp. 1–12. *In* R. K. Upadhyay, K. G. Mukerji and B. P. Chamola (eds.), *Biocontrol potential and its exploitation in sustainable agriculture: volume 2: insect pests*. Springer US, Boston, MA.
- Nghiem, L. T. P., T. Soliman, D. C. J. Yeo, H. T. W. Tan, T. A. Evans, J. D. Mumford, R. P. Keller, R. H. A. Baker, R. T. Corlett, and L. R. Carrasco. 2013. Economic and environmental impacts of harmful non-indigenous species in Southeast Asia. *PLoS One* 8: e71255.
- Nguyen, C., A. Toriello, M. Dessouky, and I. James E. Moore. 2013. Evaluation of transportation practices in the California cut flower industry. *INFORMS J. Appl. Anal.* 43: 182–193.
- Nowak, D. J., J. E. Pasek, R. A. Sequeira, D. E. Crane, and V. C. Mastro. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. *J. Econ. Entomol.* 94: 116–122.
- ODA. 2013. Oklahoma Forest Health Highlights 2013. Oklahoma Department of Agriculture, Food and Forestry, Oklahoma City, OK.
- Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in Southern New England, USA. *J. Torrey Bot. Soc.* 125: 60–73.
- Paini, D., A. Sheppard, D. Cook, P. Barro, S. P. Worner, and M. Thomas. 2016. Global threat to agriculture from invasive species. *Proc. Natl. Acad. Sci. U.S.A.* 113: 7575–7579.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52: 273–288.
- Roques, A. 2010. Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade, tourism and climate on forest biosecurity. *N. Z. J. For. Sci.* 40: 77–94.
- Sailer, R. I. 1978. Our immigrant insect fauna. *Bull. Entomol. Soc. Am.* 24: 3–11.
- Sailer, R. I. 1983. History of insect introductions, pp. 15–38. *In* C. W. Wilson and C. I. Graham (eds.), *Exotic plant pests and North American agriculture*. Academic Press, New York.
- Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. Winter, M. Arianoutsou, *et al.* 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8: 14435.
- Seebens, H., S. Bacher, T. M. Blackburn, C. Capinha, W. Dawson, S. Dullinger, P. Genovesi, P. E. Hulme, M. van Kleunen, I. Kühn, *et al.* 2021. Projecting the continental accumulation of alien species through to 2050. *Global Change Biol.* 27: 970–982.

- USDA. 2015. FY 2015 Budget summary and annual performance plan. United States Department of Agriculture, Washington, DC.
- USDA-FAS. 2021. Global Agricultural Trade System (GATS). United States Department of Agriculture, Foreign Agricultural Service, Washington, DC.
- USDOT. 2006. Freight in America: A new national picture. United States Department of Transportation, Research and Innovative Technology Administration, Bureau of Transportation Statistics, Washington, DC.
- USDOT. 2016. DOT Releases 30-Year Freight Projections. United States Department of Transportation, Research and Innovative Technology Administration, Bureau of Transportation Statistics, Washington, DC.
- USDOT. 2021. All Carrier Statistics, T-100 International Market (All Carriers). United States Department of Transportation, Bureau of Transportation Statistics, Washington, DC.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* 77: 1661–1666.
- World Bank. 2021. Air transport, passengers carried, World Development Indicators. World Bank, Washington, DC.
- WTO. 2021. International trade statistics. World Trade Organization, Geneva, Switzerland.
- Yamanaka, T., N. Morimoto, G. M. Nishida, K. Kiritani, S. Moriya, and A. M. Liebhold. 2015. Comparison of insect invasions in North America, Japan and their Islands. *Biol. Invasions* 17: 3049–3061.