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ORIGINAL PAPER

Potential establishment of alien-invasive forest insect species in the United States: where and how many?

Frank H. Koch · Denys Yemshanov · Manuel Colunga-Garcia · Roger D. Magarey · William D. Smith

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Abstract International trade is widely acknowledged as a conduit for movement of invasive species, but few studies have directly quantified the invasion risk confronting individual locations of interest. This study presents estimates of the likelihood of successful entry for alien forest insect species at more than 3,000 urban areas in the contiguous United States (US). To develop these location-specific estimates, we first utilized historical merchandise imports and insect incursions data to estimate an annual US rate of alien insect species establishment. Next, we used historical pest interception data to calculate the proportion of all insects arriving at US ports of entry that are associated with forest hosts. We then combined these results to estimate a nationwide establishment rate specifically for alien forest insects. Finally, we employed international and domestic commodity flow networks to allocate this nationwide rate to individual US urban areas. For 2010, we estimated the nationwide rate as 1.89 new alien forest insect species per year. While the establishment rates observed at most urban areas were low (<0.005 new species/year), for a few select areas the rates predict new alien forest insect species establishments every 5–15 years. This national-scale assessment provides a realistic depiction of human-assisted establishment potential in the US as well as functional inputs for quantitative models of invasion. Overall, these analyses support broad-scale biosecurity and management strategies.

Keywords Alien-invasive species · Forest pests · Human-mediated dispersal · Commodity flow · Global trade · Establishment rates

F. H. Koch (✉)
Department of Forestry and Environmental Resources, North Carolina State University, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA
e-mail: fkoch@fs.fed.us

D. Yemshanov
Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street E., Sault Ste. Marie, ON P6A 2E5, Canada

M. Colunga-Garcia
Center for Global Change and Earth Observations, Michigan State University, 205 Manly Miles Bldg., 1405 S. Harrison Rd., East Lansing, MI 48823, USA

R. D. Magarey
Center for Integrated Pest Management, North Carolina State University, 1730 Varsity Drive, Suite 300, Raleigh, NC 27606, USA

F. H. Koch · W. D. Smith
USDA Forest Service, Eastern Forest Environmental Threat Assessment Center, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

Introduction

Natural resource managers must make two types of time-sensitive decisions regarding alien-invasive species threats: those related to the potential for a new species to enter their jurisdiction, and those related to the management of a species that has already arrived (Maguire 2004). In the case of a potential new pest, effective decision making requires rapid assessment of its likely behavior and pattern of expansion, especially during the early stages of invasion. However, the risks associated with alien-invasive pests (e.g., of widespread establishment or ecological impact) are difficult to quantify as they involve interactions between factors operating across a range of spatial and temporal scales, such as the population dynamics of an invader, environmental conditions in the invaded region, and the status of potential dispersal pathways (Barney and Whitlow 2008). As an illustration of how to address some of these interactions, we developed an integrated method for estimating invasion risks and associated uncertainties for *Sirex noctilio* Fabricius, an alien forest insect recently discovered in eastern North America (Yemshanov et al. 2009a). In this study, we used a spatial stochastic model to simulate, through time, the entry of *S. noctilio* at marine ports of the United States (US) and Canada, spread of the insect from these ports as well as from previously infested locations, and the subsequent impact on its host resource (i.e., pine species). Follow-up analysis (Koch et al. 2009) revealed that parameters related to dispersal, particularly the maximum extent of dispersal, were the most important sources of uncertainty in our model system, a finding that is consistent with other studies (Nathan et al. 2003; Neubert and Caswell 2000). This finding emphasizes the fact that biological dispersal models may not adequately explain long-distance spread of invasive species, which is largely facilitated by human activities such as trade (Sakai et al. 2001). Indeed, international trade has been acknowledged as perhaps the most important conduit for the dispersal of invasive species into areas where they were previously absent, frequently across significant geographic barriers (Costello et al. 2007; Hulme et al. 2008; Kenis et al. 2009; Levine and D'Antonio 2003; Mack and D'Antonio 1998; McCullough et al. 2006; Work et al. 2005).

Despite the well recognized importance of human-mediated, long-distance dispersal in facilitating invasions, our ability to account for it in spatially explicit predictive models remains limited (Hastings et al. 2005; Yemshanov et al. 2009b). A few studies have directly modeled the relationship between trade volume and number of invasive species, but these analyses have typically been executed at broad spatial and taxonomic scales. For instance, in a global analysis across taxa, Westphal et al. (2008) concluded that a country's level of international trade (i.e., its amount of merchandise imports) is the best predictor of the number of alien invasive species found within its borders. Similarly, Hlasny and Livingston (2008) suggested that agricultural import levels are the best predictor of the number of introduced insect species in the US. However, to implement finer-scale prediction of potential entries of invasive organisms requires more detailed knowledge about the quantity, origins, and destinations of various types of imports (Hulme 2009; Hulme et al. 2008; Kenis et al. 2009). Colunga-Garcia et al. (2009), for example, used regional freight movement patterns to assess the vulnerability of US urban areas to alien forest pests. However, their approach was based solely on trade data and did not incorporate specific information about potential invasive organisms.

As a first step toward increasing our ability to characterize human-mediated dispersal, in this study we estimated annual rates of establishment in the US for a selected group of alien species (i.e., forest insects). We conducted this estimation at two spatial scales: (a) nationwide and (b) for individual urban areas across the country. Urban forests are not only vulnerable to alien-invasive species, but they also serve as critical gateways for invasions of natural forest ecosystems (Colunga-Garcia et al. 2009, 2010b; US Government Accountability Office 2006). Therefore, generating realistic estimates of the potential for human-assisted establishment at such locations should enhance the predictive capability of quantitative models of alien invasion risk such as the one described in Yemshanov et al. (2009a).

Methods

Our methodology had two primary steps. In the first step, we employed historical foreign trade and insect incursions data, as well as historical data on pest interceptions at US ports of entry, to estimate an annual rate of alien forest insect species establishment for the entire US. In the second step, we used international and domestic commodity flow networks to estimate the alien forest insect establishment rate at

>3,000 individual urban areas nationwide. To illustrate the methodology, we developed examples based on US imports of relevant commodities from throughout the world, as well as from two specific regions of origin, Europe and Asia. We selected these two regions because each is a source of prominent alien forest pests established in the US during recent decades.

Step 1: nationwide establishment rate of alien forest insect species

We began this step by using the historical trade and insect incursions data to estimate a total annual rate of alien insect species establishment (i.e., all insect species, regardless of ecological niche) for the contiguous US. Then we used the historical interception data to estimate the proportion of all insects arriving at US ports of entry that are associated with forest hosts (i.e., tree species). The results from these two analyses were subsequently multiplied to provide an estimate of the annual establishment rate of alien forest insect species in the US.

Estimating the annual US establishment rate of all alien insect species

We followed the approach of Levine and D'Antonio (2003) to derive a recent estimate of the overall annual rate of alien insect species establishment. Levine and D'Antonio (2003) estimated the number of new insect species that will be established in the US between 2000 and 2020. Specifically, they developed a set of different estimates using species-accumulation models that they applied to historical data on foreign imports and insect species incursions to the US. For our study, we re-parameterized two of their models, the log-linear species-area model and the Michaelis–Menten equation, after updating their input data—available from the National Center for Ecological Analysis and Synthesis public repository (NCEAS and D'Antonio 2008)—in a few key ways. First, we complemented the original data regarding new insect species establishments (Sailer 1983) with additional data from the North American Non-Indigenous Arthropods Database (NANIAD; see Kim and Wheeler 1991). Second, we replaced the original import values for 1999–2008 with the most recently revised numbers available (US Department of Commerce 2009b). Third, we replaced the original import projections through 2020 with new estimates that account for the recent global economic downturn and its anticipated effects on trade during the coming decade. To do so, we substituted newly available post-downturn import estimates for 2009–2010 (Nanto et al. 2009), and then adjusted the projected total values of imports for 2011–2020 downward by the average difference between the original and post-downturn totals for these 2 years (Fig. 1). Then, we converted all of the import data to 2008 dollars, including future projections, by applying inflation-adjusted conversion factors developed by Sahr (2009).

We chose to re-parameterize both the log-linear species-area and Michaelis–Menten models under the assumption that the latter, which may at times underestimate true species richness (Colwell and Coddington 1994; Palmer 1990), would provide a more conservative estimate of the annual establishment rate. We used the following form of the log-linear equation:

$$N = \log I^k + b \qquad (1)$$

where N is the number of species, I is the level of cumulative imports, k is the rate of increase in the species number, and b is a constant (Levine and D'Antonio 2003). We estimated k and b through

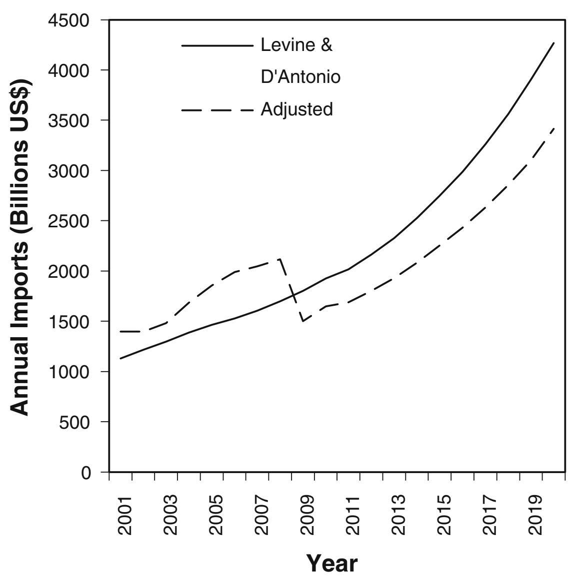

Fig. 1 Annual import curve based on data used by Levine and D'Antonio (2003) and the adjusted import curve utilized in this study. The annual import values are in 2008 US dollars

linear regression of N on log I. Similarly, we re-parameterized the following form of the Michaelis–Menten model:

$$N = \frac{N_{\max} I}{B + I} \quad (2)$$

where $N_{\max}$ (representing an upper bound on the number of species) and B are constants (Levine and D'Antonio 2003). We estimated the parameters in the Michaelis–Menten equation using the maximum likelihood method (Raajmakers 1987).

Estimating the proportion of alien insect species associated with forests

To estimate the annual rate of alien forest insect species establishment in the US, we multiplied the annual establishment rate for all alien insect species (see Eqs. 1, 2) by the proportion of species that are associated with forests. To estimate this proportion, we used the PestID database. This database, maintained by the US Department of Agriculture, Animal and Plant Health Inspection Service (APHIS), documents interceptions of alien organisms on materials arriving at US ports of entry from other countries (Magarey et al. 2009). Formerly known as the Port Information Network (PIN) database, it has been used by researchers to characterize alien pest interception patterns through time, both in general (e.g., McCullough et al. 2006) and for specific taxa such as wood- and bark-boring beetles (e.g., Haack 2001, 2006). There are several important limitations with respect to the PestID database. Most significantly, it is not a random sample; at times, various commodity categories and regions of origin have been prioritized by APHIS due to agency concerns about specific pathways and/or organisms (McCullough et al. 2006). The database also omits inspections that failed to result in detection. Despite its shortcomings, the PestID database can be a valuable tool for broad-scale analysis of historical patterns and trends (Reaser and Waugh 2007).

We analyzed all insect interceptions recorded in the database between 1984 and 2008. Following McCullough et al. (2006), we examined the database for typographical and data entry errors, then filtered the data by removing any interceptions with unknown or ambiguous origins, as well as those recorded at foreign inspection stations. We selected records from eight wood-associated families identified by APHIS for regulation under the International Standards for Phytosanitary Measures (ISPM): Cerambycidae, Buprestidae, Siricidae, Cossidae, Platypodidae, Sesiidae, Curculionidae, and Scolytidae (FAO-IPPC 2006; USDA-APHIS 2006). As previously noted by Haack (2006), many database records from Curculionidae and Scolytidae are actually associated with food items, so we only included records from these two families that were definitively associated with wood products and/or wood packing materials.

Next, we summarized the insect interceptions to create a single record for each unique insect species captured in the data. These species records represented a subsample of the available data; while a majority of the records were described to species level, approximately 45% were only described to genus, tribe, subfamily, or family. We determined the proportion of forest insect species by dividing the number of species records from the eight wood-associated insect families (i.e., including only the filtered records from Curculionidae and Scolytidae) by the total number of insect species records in the PestID database.

Step 2: urban area establishment rates of alien forest insect species

The aforementioned procedures provided us with a nationwide establishment rate for alien forest insects brought to the US via international trade. Building on the methodology outlined by Colunga-Garcia et al. (2009), we allocated this nationwide rate (i.e., the rate based on the log-linear model) to all urban areas in the contiguous US. To estimate the particular establishment rate for each urban area, we used data from the US Freight Analysis Framework (FAF), a database that describes commodity flows among US states, sub-state regions, and international trade regions (US Federal Highway Administration 2006). The most current version of the FAF (2.2) encompasses 114 US domestic trade regions (including 63 major metropolitan areas in the conterminous US), 17 additional US ports of entry not specified as domestic regions, and seven international regions of origin (Fig. 2a, b). Flows between these regions are reported, in both tonnage and monetary value, for 43 commodity categories (e.g., wood products, machinery) derived from the US-Canadian Standard Classification of Transported Goods (SCTG).

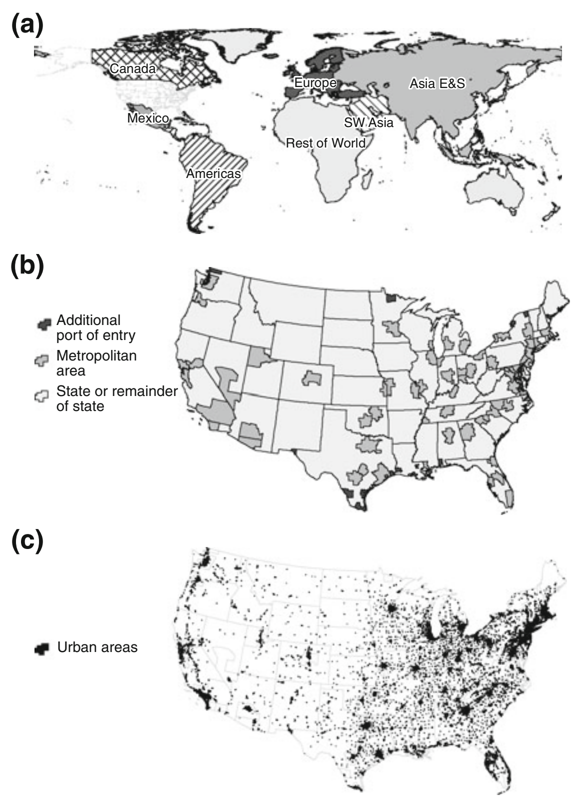

Fig. 2 **a** World regions of origin in the import/export portion of the US Freight Analysis Framework (FAF) database; **b** US regions in the domestic portion of the FAF database; **c** urban areas defined by the US Census Bureau

To combine international and domestic components of the database, Colunga-Garcia et al. (2009) classified the US FAF regions (Fig. 2b) according to their roles in the commodity flow process: (1) points-of-entry; (2) intermediate destinations; and (3) final destinations. "Points-of-entry" are locations where imports initially arrive in the US, as recorded in the import/export portion of the FAF database. In turn, regions specified as import destinations in the import/export portion of the database represent "intermediate destinations", under the assumption that imported commodities will become part of the domestic commodity flow upon entering the US. Hence, "final destinations" are the regions where the imports presumably arrive after domestic transport (i.e., from the intermediate destinations).

Colunga-Garcia et al. (2009) calculated F_k, the tonnage of a selected import commodity that reaches the kth final destination region, as follows:

$$F_k = \sum_{j=1}^{n} \left[\frac{D_{jk}}{TD_j} \sum_{i=1}^{m} I_{ij} \right] \quad (3)$$

where I_{ij} is the tonnage of the selected FAF commodity that is transported from the ith point-of-entry to the jth intermediate destination region; D_{jk} is the tonnage of the selected commodity that is transported from the jth intermediate destination region to the kth final destination region; TD_j is the total tonnage of the selected commodity that is transported from the jth intermediate destination region; m is the number of points-of-entry; and n is the number of intermediate destination regions. In this equation, import and domestic commodity flow data are pooled across transport modes.

We adapted Eq. 3 to account for differences between world regions of origin in terms of serving as sources of alien forest insects, which is distinct from those regions' relative contributions to total US imports. For example, although the US imports a substantial quantity of commodities from Canada, the number of alien forest insects intercepted at US ports of entry that come from Canada is very small; this may perhaps be explained by the high degree of integration between the two countries in terms of pest surveillance and regulatory policies, as well as the fact that many species already occur in both countries (Haack 2001). We used the PestID database to calculate the proportion of forest insect taxa (i.e., including interceptions specified only to genus, tribe, subfamily, or family) historically linked to each region of origin (Table 1). This was a departure from our earlier analysis using the PestID database, where

Table 1 Proportion of the unique forest insect taxonomic identities in the PestID database associated with each world origin region

Region of origin	Proportion	Weight, w_h
Americas	0.17	0.36
Asia E&S	0.21	0.45
Canada	0.01	0.02
Europe	0.48	1
Mexico	0.07	0.14
Rest of World	0.04	0.09
SW Asia	0.01	0.02

The corresponding weights were used to adjust the commodity import tonnages from each region (see Eq. 4) we considered only definitively identified species; in this case, we wanted to minimize biases due to differing levels of taxonomic knowledge about the origin regions (i.e., more forest insects may be known from certain origin regions, making it more likely that intercepted specimens can be identified to species level). We converted the regional proportions into weights, which we applied when calculating F_{kl}, the "adjusted" tonnage of imports of a given commodity l that reaches the kth final destination region:

$$F_{kl} = \sum_{j=1}^{n} \left[\frac{D_{jk}}{TD_j} \sum_{i=1}^{m} \sum_{h=1}^{p} w_h I_{hij} \right] \quad (4)$$

where I_{hij} is the tonnage of the selected commodity imported from the hth world region of origin to the ith point-of-entry and subsequently transported to the jth intermediate destination region; w_h is the weight assigned to the hth origin region (from Table 1); and p is the number of world regions being analyzed. All other terms are identical to those specified in Eq. 3.

Several commodity categories are pertinent with respect to the introduction and transport of alien forest insects (Table 2). Logically, imported logs are a significant source of forest invaders (Piel et al. 2008, 2005), but solid wood packing materials (SWPM) associated with many imported commodity types (Table 2) have also historically served as an important source (Brockerhoff et al. 2006; Haack 2001, 2006; McCullough et al. 2006; Work et al. 2005). Ideally, we would have accounted for the proportion of the imported tonnage of a given commodity that is typically composed of wood materials. Because this information was not available for our study, we assumed that 100% of the imported tonnage in the categories "logs and other wood in the rough" and "wood products" could harbor forest insects, but that only 10% of the imported tonnage in our other categories of interest represented materials that may harbor these insects. We applied these weights in a new equation for estimating F_k, which in this case represents the adjusted FAF tonnage from multiple commodity categories of interest that reaches the kth final destination region:

$$F_k = \sum_{l=1}^{q} w_l F_{kl} \quad (5)$$

where F_{kl} is the tonnage of an individual commodity l estimated to reach the kth final destination (from Eq. 4); w_l is the weight associated with commodity category l (from Table 2); and q is the number of commodity categories being analyzed (13 in this study).

We estimated U_{kz}, the import tonnage that is expected to reach the zth urban area within the kth final destination region, as follows (Colunga-Garcia et al. 2009):

Table 2 FAF database commodity categories associated with transport of forest insects

SCTG code	Commodity category	Weight, w_l
10	Monumental or building stone	0.1
25	Logs and other wood in the rough	1
26	Wood products	1
31	Nonmetallic mineral products	0.1
32	Base metal in primary or semi-finished forms and in finished basic shapes	0.1
33	Articles of base metal	0.1
34	Machinery	0.1
35	Electronic and other electrical equipment and components and office equipment	0.1
36	Motorized and other vehicles (including parts)	0.1
37	Transportation equipment, not elsewhere classified	0.1
38	Precision instruments and apparatus	0.1
39	Furniture, mattresses and mattress supports, lamps, lighting fittings	0.1
40	Miscellaneous manufactured products	0.1

Categories are derived from the US-Canadian Standard Classification of Transported Goods (SCTG). The weights (see Eq. 5) reflect the estimated proportion of import shipment tonnage within a particular commodity category that may harbor forest insects (i.e., the portion of the shipment comprised of wood, including pallets, crates, and other packing materials)

$$U_{kz} = F_k \left[\frac{P_{kz} T_{kz}}{\sum_{z=1}^{N} P_{kz} T_{kz}} \right] \quad (6)$$

where F_k is the import tonnage expected to reach the kth final destination region (in this case, the adjusted tonnage from Eq. 5); P_{kz} is the human population in the zth urban area of the kth final destination region; T_{kz} is the maximum truck flow to the zth urban area of the kth final destination region; and N is the number of urban areas found within the kth final destination region. We delineated urban areas using a geospatial data layer from the US Census Bureau (Fig. 2c) that was accompanied by corresponding human population data (i.e., P_{kz} values). We then intersected this layer with FAF Highway Link and Truck Traffic data in order to assign each urban area the maximum truck flow value, T_{kz}, observed among the FAF highway segments that fell within it (specifics on this approach, including data sources, are documented in Colunga-Garcia et al. 2009).

To estimate the annual alien forest insect species establishment rate for each urban area, we converted the U_{kz} values into proportions by dividing them by the total adjusted tonnage from all origin regions, which we then multiplied by the nationwide forest insect establishment rate based on the log-linear model (see "Methods" for Step 1). We developed separate urban-area establishment rate estimates using FAF import projections for 2010 and 2020 (US Federal Highway Administration 2006) as well as the mean annual nationwide establishment rates for 2001–2010 and 2011–2020, respectively. In addition to estimating rates based on imports from all world regions of origin, we were also interested in differences between establishment patterns associated with specific origin regions. To illustrate such differences, we calculated the rates based only on imports from two individual regions, Europe and Asia (i.e., the FAF origin region "Asia E&S").

Results

Nationwide establishment rate of alien forest insect species

The two species-accumulation models used to estimate establishment rates for all alien insect species performed similarly in describing the historical data, with $R^2 = 0.97$ for the log-linear model and $R^2 = 0.98$ for the Michaelis–Menten model (Table 3; Fig. 3). The two models diverge in terms of the predicted number of new insect species establishments, with the log-linear model predicting 3–5 times higher establishment rates than the Michaelis–Menten equation (Table 3). For both models, the mean annual establishment rate for 2011–2020 is lower than the mean rate predicted for the previous decade, 2001–2010. This is expected since both model curves, especially the Michaelis–Menten curve, appear to begin leveling off within the upper range of the historical data (Fig. 3). Furthermore, the downward-adjusted import forecasts for 2011–2020 (i.e., after accounting for the global economic downturn of the past few years) inevitably had a dampening effect on the predicted rate of new establishments. Nevertheless, even the more conservative Michaelis–Menten model estimates that approximately four new alien insect species will be established annually in the US during the coming decade. With respect to the PestID database, our determination that 3.17% of the recorded insect interceptions on cargo were associated with forest insects (Table 4) is similar to McCullough et al. (2006), who reported that insect interceptions in wood products represented 3.65% of all insect interceptions on cargo during the period 1984–2000.

Combining the results from the re-parameterized log-linear model (Table 3) and the PestID proportional analysis (Table 4), the mean annual rate of alien forest insect species establishment in the US is

Table 3 Summary of the re-parameterized species-import models

Model	Fitted equation	R^2	Predicted annual insect species establishment rate	
			2001–2010[a]	2011–2020[a]
Log-linear species-area	$N = \log I^{978.79257} - 11176$	0.97	20.4	18.3
Michaelis–Menten	$N = \frac{2015.4I}{2.76\times10^{12}+I}$	0.98	6.5	3.9

[a] Mean annual establishment rate over the decade

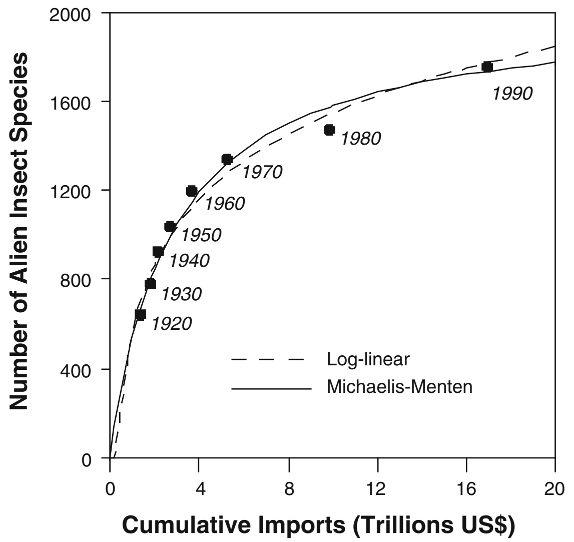

Fig. 3 Re-parameterized log-linear and Michaelis–Menten models relating cumulative US imports to the establishment of alien insect species. The cumulative import values are in 2008 US dollars

Table 4 Summary of insect interceptions on cargo from the PestID database

Summarization level	All insects	Forest insects[a]
Individual interception records	436,511	13,834 (3.17%)
Unique species	3,443	319 (9.27%)

[a] Number in parentheses is the percentage, for each row, of all insects classified as forest insects

estimated to be 1.89 species per year for the period 2001–2010 and 1.7 species per year for 2011–2020. Utilizing the re-parameterized Michaelis–Menten model instead of the log-linear, the annual rate is estimated to be 0.6 species per year for 2001–2010 and 0.36 species per year for 2011–2020. Notably, even these far more conservative estimates suggest that we can expect a new alien forest insect species to become established somewhere in the US every 2–3 years. If we apply the "tens rule" of Williamson and Fitter (1996) to our estimates (i.e., 10% of newly established species will become invasive pests that causes significant ecological and/or economic damages), this suggests that one new alien insect species will emerge as a significant pest of US forests approximately every 5–6 years (i.e., assuming annual rates of 0.19 and 0.17 species per year for 2001–2010 and 2011–2020, respectively, based on the log-linear model). This appears consistent with recent US history, which has seen the emergence of at least four ecologically and/or economically significant alien forest insects during the past 20–25 years: the emerald ash borer (*Agrilus planipennis*); the Asian longhorned beetle (*Anoplophora glabripennis*); the sirex woodwasp (*Sirex noctilio*); and the redbay ambrosia beetle (*Xyleborus glabratus*).

Urban area establishment rates of alien forest insect species

For 2010 (Fig. 4a) and 2020 (Fig. 4b), the top two urban areas (out of 3,126) in terms of establishment rate of alien forest insect species, when considering relevant commodity imports from all origin regions, were Los Angeles–Long Beach–Santa Ana, CA and New York–Newark, NY-NJ-CT. For both years, the predicted rates for Los Angeles–Long Beach–Santa Ana are substantially higher than the rates for any other US urban area (Table 5). The rate estimates for this area essentially mean that a new alien forest insect species would become established every 4–5 years. The estimated rates for the next highest-ranked urban area, New York–Newark, project the establishment of a new forest insect species every 8–9 years. For Houston, TX (the third highest-ranked urban area), the calculated establishment rates suggest that a new forest insect will be established approximately every 13–15 years. There is a notable drop-off in the rates estimated for all other urban areas, with none exhibiting a rate above 0.041 new species per year (i.e., one new species every ≈ 24 years).

Generally, the urban areas display only minor changes in their predicted establishment rates from 2010 to 2020 (Table 5; Fig. 4). In a few cases (Los Angeles–Long Beach–Santa Ana; San Diego, CA; Riverside-San Bernardino, CA), the predicted establishment rates show an increase. In the case of San Francisco-Oakland, CA, the establishment rate is predicted to remain essentially flat between 2010 and 2020 (although its ranking is projected to increase relative to other urban areas). The rest of the top 25 urban areas show decreases in establishment rate between 2010 and 2020 (Table 5). Overall, 49 (1.6%) urban areas exhibited at least minor rate increases between 2010 and 2020, nearly all of which were in California, except for Las Vegas and two other urban areas in Nevada (Fig. 4a, b).

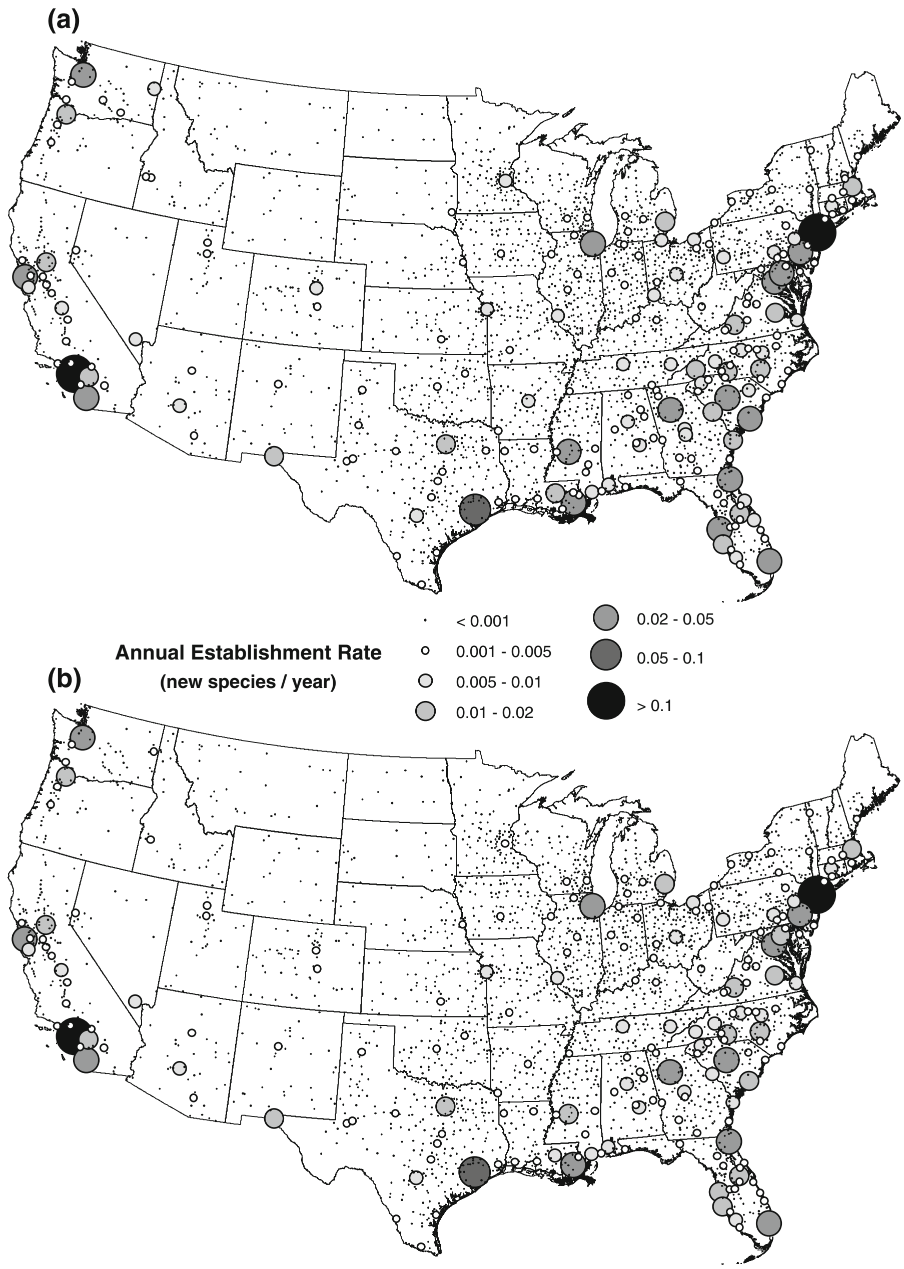

Fig. 4 Annual alien forest insect species establishment rates in US urban areas, based on imports of relevant commodities from all world regions of origin: **a** rates estimated using 2010 FAF projections and the 2001–2010 mean annual rate of alien forest insect establishment for the US (1.89 species/year from the log-linear species-accumulation model); **b** rates estimated using 2020 FAF projections and the 2011–2020 mean annual rate for the US (1.7 species/year from the log-linear model)

Growth of Asian imports appears to drive this increase in the projected establishment rates in California (Table 6). Four of the top 10 US urban areas in terms of the establishment rate for Asian forest insect species are those mentioned in the previous paragraph: Los Angeles–Long Beach–Santa Ana, San Diego, San Francisco–Oakland, and Riverside–San Bernardino (Table 6). For all of them, the Asian species establishment rate is projected to increase 6–8% between 2010 and 2020. The most likely destination for Asian forest insects is the Los Angeles–Long Beach–Santa Ana area, where the

Table 5 Top 25 US urban areas in terms of the annual establishment rate of alien forest insect species transported from all world regions (i.e., from all FAF origin regions)

	Urban Area	2010 Annual rate	2020 Annual rate[a]
1	Los Angeles–Long Beach–Santa Ana, CA	0.238	0.250 (1)
2	New York–Newark, NY–NJ–CT	0.121	0.106 (2)
3	Houston, TX	0.079	0.069 (3)
4	Seattle, WA	0.041	0.038 (4)
5	Miami, FL	0.040	0.035 (6)
6	Philadelphia, PA–NJ–DE–MD	0.038	0.032 (7)
7	San Diego, CA	0.035	0.037 (5)
8	Washington, DC–VA–MD	0.031	0.028 (8)
9	Atlanta, GA	0.031	0.027 (10)
10	Columbia, SC	0.030	0.025 (12)
11	Chicago, IL–IN	0.029	0.027 (11)
12	San Francisco–Oakland, CA	0.028	0.028 (9)
13	New Orleans, LA	0.027	0.022 (14)
14	Jacksonville, FL	0.027	0.023 (13)
15	Charleston–North Charleston, SC	0.023	0.019 (16)
16	Tampa–St. Petersburg, FL	0.022	0.020 (15)
17	Baltimore, MD	0.022	0.018 (17)
18	Jackson, MS	0.021	0.016 (18)
19	Roanoke, VA	0.017	0.014 (22)
20	Dallas–Fort Worth–Arlington, TX	0.017	0.016 (19)
21	Portland, OR–WA	0.017	0.016 (20)
22	Fayetteville, NC	0.015	0.012 (23)
23	Riverside–San Bernardino, CA	0.014	0.015 (21)
24	El Paso, TX–NM	0.014	0.012 (24)
25	Charlotte, NC–SC	0.013	0.011 (25)

Rates are based on FAF import projections for the years in question as well as species-accumulation estimates from the log-linear model

[a] Number in parentheses is the urban area's ranking based on the 2020 annual rate

Asian species establishment rate accounts for 84% of the total species establishment rate in 2010 and 85% in 2020. This means that we could potentially expect the establishment of an alien forest insect species originating specifically from Asia every 4–5 years. A number of urban areas outside California (such as New York–Newark or Seattle) have Asia as a prominent source of alien forest insects (Table 6; Fig. 5a). Still, all urban areas outside California and Nevada are predicted to have a decrease in both the Asian species and overall species establishment rates between 2010 and 2020.

Europe is a more prominent contributor to the species establishment rates predicted for eastern US urban areas. In fact, Europe typically accounts for 50–60% of the total establishment rate in urban areas near the US Atlantic coast (Table 7; Fig. 5b). The most likely destination for European forest insects is the New York–Newark area, where a forest insect species from this origin region is predicted to be established every 15–17 years. Houston is the next highest-ranked urban area, with a new European species predicted to be established every ≈ 30 years. In addition, Europe is a moderately significant source for the Los Angeles–Long Beach–Santa Ana area. Outside of these three areas, no other US urban area exhibits a predicted European species establishment rate greater than 0.018 species per year (i.e., the 2010 rate for Columbia, SC and Miami, FL). Nevertheless, for many eastern US cities, potential European invaders will continue be a slightly more important concern than potential Asian invaders in the coming decade.

Discussion

Three major findings from our analysis have implications for research and management. First, under current and projected US import patterns, an average of ≈ 2 alien forest insect species are predicted to be

Table 6 Top 25 US urban areas in terms of the annual establishment rate of alien forest insect species transported from Asia (i.e., from FAF origin region "Asia E&S")

	Urban area	2010 Annual rate	% 2010 Total rate[a]	2020 Annual rate[b]	% 2020 Total rate[a]
1	Los Angeles–Long Beach–Santa Ana, CA	0.200	84	0.214 (1)	85
2	New York–Newark, NY–NJ–CT	0.037	31	0.033 (2)	31
3	Seattle, WA	0.034	82	0.032 (3)	83
4	San Diego, CA	0.028	79	0.03 (4)	80
5	New Orleans, LA	0.017	62	0.014 (7)	62
6	Houston, TX	0.017	21	0.015 (6)	22
7	San Francisco–Oakland, CA	0.016	57	0.017 (5)	61
8	Philadelphia, PA–NJ–DE–MD	0.014	37	0.012 (9)	38
9	Jackson, MS	0.013	62	0.01 (10)	61
10	Riverside–San Bernardino, CA	0.012	84	0.013 (8)	85
11	Atlanta, GA	0.011	36	0.01 (11)	37
12	Portland, OR–WA	0.010	57	0.009 (12)	59
13	Chicago, IL–IN	0.009	30	0.009 (13)	32
14	Washington, DC–VA–MD	0.008	26	0.007 (14)	26
15	Sacramento, CA	0.006	56	0.006 (15)	57
16	Roanoke, VA	0.006	35	0.005 (21)	35
17	Miami, FL	0.006	15	0.005 (17)	16
18	Columbia, SC	0.006	19	0.005 (20)	20
19	Las Vegas, NV	0.006	72	0.006 (16)	74
20	Baton Rouge, LA	0.005	48	0.004 (23)	47
21	Dallas–Fort Worth–Arlington, TX	0.005	31	0.005 (19)	31
22	Baltimore, MD	0.005	23	0.004 (24)	24
23	Jacksonville, FL	0.005	18	0.004 (22)	19
24	San Jose, CA	0.005	57	0.005 (18)	61
25	Gulfport–Biloxi, MS	0.005	62	0.004 (27)	61

Rates are based on FAF import projections and species-accumulation estimates from the log-linear model

[a] Percentage of the total annual species establishment rate (Table 5) attributed to Asia

[b] Number in parentheses is the urban area's ranking based on the 2020 annual rate

established somewhere in the US every year, and a significant forest insect pest is predicted to be established every 5–6 years. These rates may not seem high, but it is important to consider that just one established species could potentially have an economic impact on the order of tens of millions, or even billions, of US dollars (e.g., Nowak et al. 2001). While it is somewhat difficult to validate our rate estimates using recent occurrence data, especially given the lag time between species arrival and first discovery (Costello and Solow 2003), available information suggests that our estimates approximate reality. For instance, Mattson et al. (1994) listed 368 alien insect species that were known to feed on woody plants in the US and Canada, virtually all of which can be presumed to have arrived after 1800 (Liebhold et al. 1995). This number of species, invading over a nearly 200-year period, translates to an annual establishment rate which is quite similar to what we have estimated in this study, although Mattson et al. (1994) did include some species found exclusively in Canada or on nursery plants. In terms of significant pests, we already noted four forest insect species that have emerged in the US during the past 20–25 years (see "Results"), which generally agrees with our rate estimate. Admittedly, the long-term impacts of some of these species are uncertain, and other recent arrivals (e.g., Mediterranean pine engraver, *Orthotomicus erosus*) currently considered to be secondary pests may eventually become major pests in the US (Haack 2004). We acknowledge these uncertainties, but feel justified in utilizing our nationwide rate estimates for the subsequent steps of our analysis.

Second, considering worldwide imports to the US, the two urban areas most likely to see alien forest insects become established are Los Angeles–Long

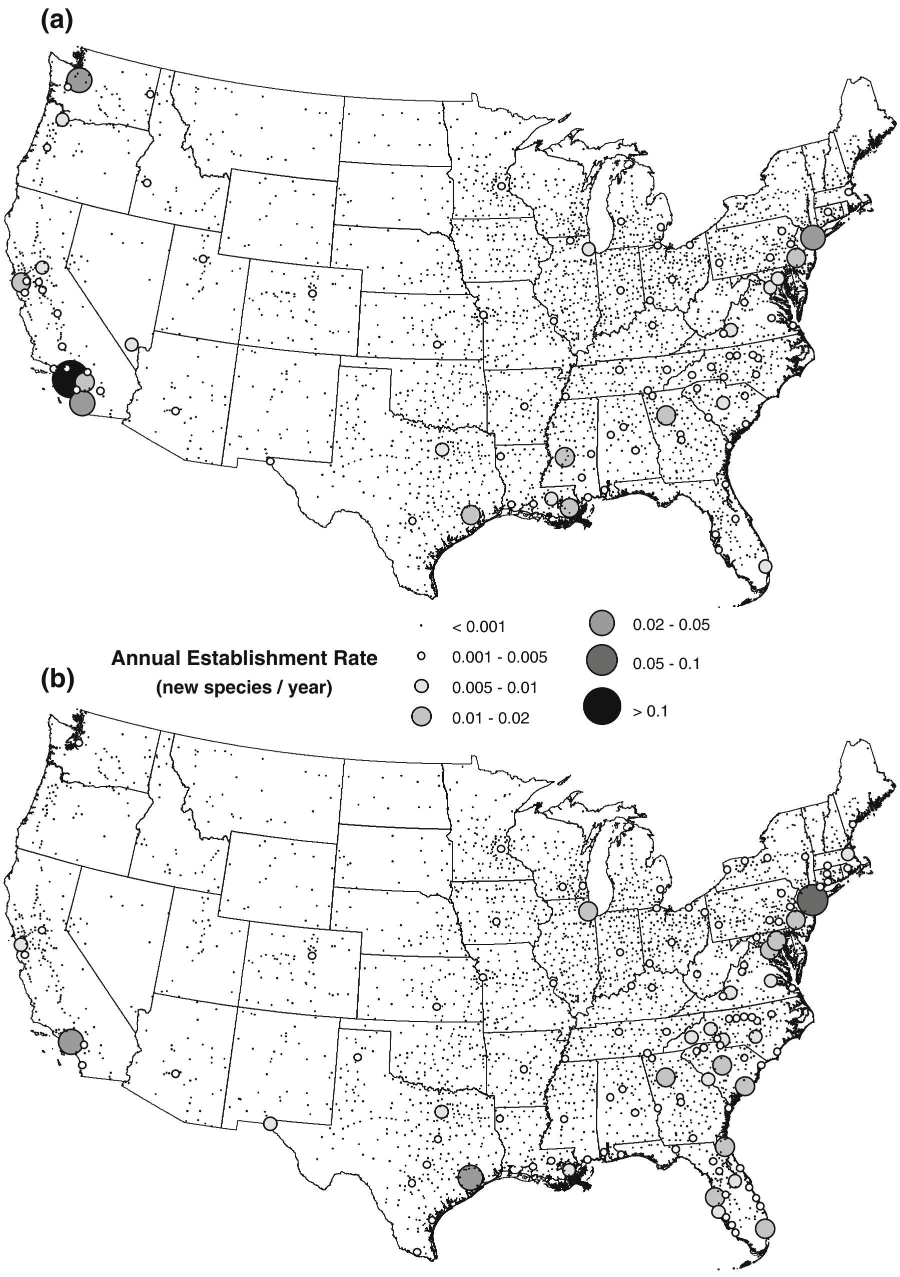

Fig. 5 Annual forest insect establishment rates in US urban areas, based on imports of relevant commodities from a specific origin region: **a** Asia (i.e., FAF region "Asia E&S"); **b** Europe. Rates were estimated using 2010 FAF projections and the 2001–2010 mean annual rate of alien forest insect establishment for the US (1.89 species/year from the log-linear model)

Beach–Santa Ana and New York–Newark. These are the two most populous US urban areas, and both also serve as important marine ports of entry; in fact, the ports of Los Angeles, Long Beach, and New York are the nation's three busiest shipping container facilities (US Army Corps of Engineers 2010). Due to their population size and the corresponding demand for goods and materials, a substantial proportion of their imports simply remains in each of two urban areas, which results in their relatively high predicted

Table 7 Top 25 US urban areas in terms of the annual establishment rate of alien forest insect species transported from Europe

	Urban area	2010 Annual rate	% 2010 Total rate[a]	2020 Annual rate[b]	% 2020 Total rate[a]
1	New York–Newark, NY–NJ–CT	0.069	57	0.06 (1)	56
2	Houston, TX	0.037	47	0.032 (2)	47
3	Los Angeles–Long Beach–Santa Ana, CA	0.022	9	0.021 (3)	8
4	Columbia, SC	0.018	60	0.015 (5)	60
5	Miami, FL	0.018	46	0.016 (4)	45
6	Washington, DC–VA–MD	0.016	52	0.015 (6)	52
7	Philadelphia, PA–NJ–DE–MD	0.014	37	0.012 (8)	36
8	Charleston–North Charleston, SC	0.014	60	0.011 (9)	60
9	Jacksonville, FL	0.014	52	0.012 (7)	51
10	Atlanta, GA	0.012	40	0.011 (10)	40
11	Chicago, IL–IN	0.012	39	0.011 (11)	39
12	Tampa–St. Petersburg, FL	0.011	49	0.01 (12)	48
13	Baltimore, MD	0.011	48	0.009 (13)	48
14	Fayetteville, NC	0.009	60	0.007 (14)	59
15	Roanoke, VA	0.009	50	0.007 (15)	50
16	Charlotte, NC–SC	0.007	54	0.006 (16)	53
17	Sarasota–Bradenton, FL	0.007	58	0.006 (17)	57
18	Asheville, NC	0.007	60	0.005 (18)	59
19	New Orleans, LA	0.006	23	0.005 (23)	23
20	Richmond, VA	0.006	51	0.005 (22)	51
21	Orlando, FL	0.006	48	0.005 (19)	47
22	Boston, MA–NH–RI	0.006	46	0.005 (24)	45
23	Hickory, NC	0.006	60	0.005 (25)	59
24	Dallas–Fort Worth–Arlington, TX	0.006	34	0.005 (21)	33
25	El Paso, TX–NM	0.005	39	0.005 (26)	38

Rates are based on FAF import projections and species-accumulation estimates from the log-linear model

[a] Percentage of the total annual species establishment rate (Table 5) attributed to Europe

[b] Number in parentheses is the urban area's ranking based on the 2020 annual rate

establishment rates. In fact, most urban areas in the top 25 (Table 5) also serve as marine ports of entry, though there are some exceptions: Atlanta, GA; Columbia, SC; Jackson, MS; Roanoke, VA; Dallas–Fort Worth–Arlington, TX; Roanoke, VA; Fayetteville, NC; Riverside–San Bernardino, CA; El Paso, TX–NM; and Charlotte, NC. While El Paso is a major through-point for commodities imported from Mexico, the rest of these areas represent populous and/or highly connected nodes in the domestic commodity transport network.

Our third major finding is that urban areas of California are more likely to experience an increase in the number of establishments of forest species from Asia between 2010 and 2020. Urban areas in the eastern US are generally more vulnerable to forest species from Europe, although the number of establishments is projected to decrease. Our establishment rate allocation method uses import tonnages as an indirect measure of propagule pressure (Kolar and Lodge 2001; Lockwood et al. 2005). One aspect of this indirectness is that equal-tonnage shipments from different regions of origin may not necessarily produce similar propagule pressure. We assumed that the historic interceptions data (i.e., the PestID data) would provide a realistic characterization of the relative contributions of the individual origin regions to the total level of forest insect propagule pressure facing the US. Significantly, the interceptions data show Europe as the most prominent source of alien forest insects detected at US ports of entry. Indeed, about 75% of the alien insect species currently living on trees and shrubs in North America are endemic to Europe (Gandhi and Herms 2010; Mattson et al. 2007). The high level of trade and the biogeographical similarity between Europe and North America

(Mattson et al. 2007) may continue to facilitate introductions of forest insects from Europe to the US in the future. Nonetheless, our findings suggest that, during the next few decades, there could be a shift towards a greater proportion of forest invaders originating in Asia, especially given our current level of trade with China and other Asian countries (US Department of Commerce 2009a). This appears to be most relevant for California. We are currently exploring data sources that may help us determine appropriate regional weights for future rate estimates.

There are some issues that should be considered for further research. First, it is worth noting that both species-accumulation models display a decrease in the rate of new species establishments during recent decades (Fig. 3). This may support the idea advanced by some researchers (Belmaker et al. 2009; Wonham and Pachepsky 2006) that the pool of potential new invaders inevitably gets smaller as more species become established in the area of interest. Clearly, this has ramifications for future estimates of alien species establishment rates, and so it would be beneficial to have more recent establishment data so that we could determine if the apparent trend continues. Unfortunately, the NANIAD database has not been regularly updated since the mid-1990s, although it may be possible to compile recent data from other sources (e.g., the New Pest Advisory Group, which is affiliated with APHIS). This will be a focus of future work.

Second, like shipments from different origin regions, individual commodity categories may have different capacities for supporting and transporting alien organisms. For this study, we adopted a simplified weighting system where we assigned the highest transport potential (i.e., 100%) to raw wood commodities, but assumed that shipments of other manufactured commodities would include 10% low-quality wood packing materials such as crating, pallets, and dunnage. Unfortunately, we had to base this latter weight on very limited data. Molina-Murillo et al. (2005), studying containerized exports from the US, estimated that the typical 20-foot shipping container (i.e., one ton-equivalent unit, or TEU) contained 20.75 pallets, which translates to roughly 2% of the shipment tonnage at capacity. After allowing for all of the additional wood packing materials associated with commodity shipments (e.g., crates, bins, drums, spacers, and dunnage), we think 10% is a reasonable estimate, but admit that this, like our other assumptions, comes with some degree of uncertainty. More precise estimates of the commodities' transport potential could considerably improve the accuracy of the estimates of establishment rates for individual urban areas, although they may not change the overall rate patterns presented in this study.

Third, we have already mentioned the challenge of validating the results of our analysis based on recent anecdotal evidence, and this extends to our rate estimates for individual urban areas. Intuitively, it seems that urban areas with limited natural forest (e.g., Los Angeles–Long Beach–Santa Ana) would be unable to support many new forest insect establishments. However, a critical factor to consider is that urban areas may have higher tree species diversity than nearby natural forests, primarily due to the planting of non-native trees (Nowak 1994). This may provide adequate host for invaders that would not otherwise become successfully established. For instance, species from the *Eucalyptus* genus, which are native to Australia and New Guinea, are widely planted in California urban areas. Significantly, Paine et al. (2000) asserted that ≈ 15 new pests of *Eucalyptus* species were introduced into California between 1984 and 2000. In short, determining the true alien forest insect establishment potential for a given urban area is likely to require collection and analysis of a detailed urban tree inventory. This could be a demanding task, although such data might prove useful in a number of regards (e.g., for estimating an area's level of carbon sequestration).

Within an urban area, the abundance and connectivity of host tree stands will ultimately determine where an alien forest insect species becomes successfully established. Unfortunately, the coarse resolution of the FAF data and lack of information on specific transport pathways preclude analysis of possible establishment hot spots within urban areas. One possible strategy for identifying such hot spots is to link moderate-resolution maps of tree cover with a measure of propagule pressure such as human population size or amount of commercial/industrial land area (Colunga-Garcia et al. 2010a). Alternatively, access to highly detailed transportation data (such as roadside survey records and traffic load data for individual road segments collected by state and federal Departments of Transportation) would allow for more precise mapping of the commodity flows along major regional transportation corridors, and perhaps even some local corridors. Linking the directional road survey information with data on the geographic distribution of human settlements, potential markets, and the abundance of susceptible hosts would ultimately provide more accurate estimates of the local pest establishment potential at urban locations nationwide.

Management implications

We should note that our results presume that current international rules for treatment of wood and wood packing materials (i.e., International Standards for Phytosanitary Measures No. 15, or ISPM 15) will only have a modest impact on the rate of wood-associated insects establishing in the US through time (FAO-IPPC 2006). Actually, ISPM 15 was adopted by Canada and the US only recently, and was always intended to reduce, rather than eliminate, introduction risk. Furthermore, there has been some skepticism regarding its effectiveness, which may be compromised by fraudulent practices and/or treatment failures (Reaser et al. 2008; Reaser and Waugh 2007). Notably, a recent study (Haack and Petrice 2009) reported that a small percentage of ISPM 15-compliant wood items surveyed at six US ports contained live insects of quarantine significance. Whether or not ISPM 15 proves effective at reducing risk, it is important to consider that US import volumes, after recovering from the current global economic downturn, are likely to expand rapidly in the same manner as they have historically, such that the forest insect establishment rate could still be high in coming decades.

Predicting which alien organisms are most likely to become significant pests is an appropriate starting point when developing an effective invasive species management strategy (Kolar and Lodge 2001; Reichard and Hamilton 1997). Yet, many species do not immediately emerge as threats to the places they invade (Crooks 2005; Williamson and Fitter 1996). Thus, it is also advisable to have a system that anticipates where and at what rate invaders from taxa of interest are most likely to be established, thus offering a way to prioritize border control efforts (e.g., commodity inspections), post-border surveillance, and rapid-response measures (Magarey et al. 2009; Meyerson and Reaser 2002). The analysis presented here has immediate relevance to decision makers responsible for implementing forest biosecurity strategies. Furthermore, the establishment-rate geographic patterns captured in this study can serve as key input data for subsequent assessments of the introduction, spread, and potential impacts of alien forest insect species. One feature of our two-step methodology is that it goes beyond tonnage allocation, which is essentially a framework for representing relative propagule pressure, to more directly estimate actual propagule pressure for a particular target group, alien forest insect species. The methodology is fairly generic, and so we believe it can be readily adapted for other, non-forest sectors (such as agriculture and horticulture). In addition, the approach could be modified to analyze other dispersal pathways such as air passenger transport, which has been increasingly recognized for its role in the movement of alien species (Hulme 2009; Liebhold et al. 2006; Tatem 2009).

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