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RESEARCH PAPER

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Spatial patterns of discovery points and invasion hotspots of non-native forest pests

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Abstract

Aim: Establishments of non-native forest pests (insects and pathogens) continue to increase worldwide with growing numbers of introductions and changes in invasion pathways. Quantifying spatio-temporal patterns in establishment locations and subsequent invasion dynamics can provide insight into the underlying mechanisms driving invasions and assist biosecurity agencies with prioritizing areas for proactive surveillance and management.

Location: United States of America.

Time period: 1794–2018.

Major taxa studied: Insecta, plant pathogens.

Methods: Using locations of first discovery and county-level occurrence data for 101 non-native pests across the contiguous USA, we (a) quantified spatial patterns in discovery points and county-level species richness with spatial point process models and spatial hotspot analyses, respectively, and (b) identified potential proxies for propagule pressure (e.g., human population density) associated with these observed patterns.

Results: Discovery points were highly aggregated in space and located in areas with high densities of ports and roads. Although concentrated in the north-eastern USA, discovery points also occurred farther west and became less aggregated as time progressed. Invasion hotspots were more common in the north-east. Geographic patterns of discovery points and hotspots varied substantially among pest origins (i.e., global region of pests' native ranges) and pest feeding guilds. Significant variation in invasion richness was attributed to the patterns of first discovery locations. Data and shapefiles comprising analyses are provided.

Main conclusions: Use of spatial point pattern analyses provided a quantitative characterization of the central role of human activities in establishment of non-native pests. Moreover, the decreased aggregation of discovery points through time suggests that invasion pathways to certain areas in the USA have either been created or intensified by human activities. Overall, our results suggest that spatio-temporal variability in the intensity of invasion pathways has resulted in marked geographic patterns of establishment and contributed to current macroscale patterns of pest invasion in the USA.

KEYWORDS

Getis–Ord, Insecta, invasion biology, pathogens, pathways, Ripley's *K* function, spatial point process

1 | INTRODUCTION

Biological invasions can be categorized into three phases: arrival, establishment and spread (Liebhold & Tobin, 2008). For invasive forest pests (insects and pathogens), the first phase is typically facilitated by inadvertent human transportation, for example, through importation of live plants, wood packaging material, or timber (Brockerhoff & Liebhold, 2017; Liebhold, Brockerhoff, Garrett, Parke, & Britton, 2012; Skarpaas & Økland, 2009). The arrival of non-native pests has increased with international trade and travel (Levine & D'Antonio, 2003; Turbelin, Malamud, & Francis, 2016) and more conspecifics arriving per unit of time and/or space (i.e., higher propagule pressure) increases the likelihood that a species will locate resources and overcome demographic barriers to establishment (Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009). The final invasion phase, spread, is affected by human activities (e.g., movement of pests within the invaded range; Gilbert, Grégoire, Freise, & Heitland, 2004; Shigesada & Kawasaki, 1997), variation in habitat quality (Hudgins, Liebhold, & Leung, 2017; Liebhold et al., 2013), temperature (Lantschner et al., 2014), voltinism (Fahrner & Aukema, 2018), time since establishment (Andow, Kareiva, Levin, & Okubo, 1990) and other factors. Processes operating during each phase combine to determine the extent of currently invaded ranges.

The number of non-native forest pests arriving and establishing in the USA continues to increase (Aukema et al., 2010). Non-native pests impact forest structure and succession (Liebhold et al., 2017; Lovett et al., 2016; Morin & Liebhold, 2015) and cause billions of dollars (US$) in economic impacts per annum (Aukema et al., 2011). Given that human activity drives pest arrival and establishment, discovery of pests in densely populated or well-travelled regions may be expected (Huang, Zhang, Kim, & Suarez, 2012). Locations of arrival and establishment can vary temporally with changes in international trade, such as fluctuations in economic markets that alter the intensity of invasion pathways between regions (Everett, 2000) or as human population densities change in time and space. However, spatial correlates of discovery points for non-native forest pests in the USA have not been quantified.

The USA is highly invaded by forest pests with the number of non-native species per unit area ("invasion richness") distributed heterogeneously across the country (Liebhold et al., 2013). The geographic distribution of locations of initial invader establishment likely contributes to macroscale patterns of invasion richness, as pests spread into adjacent areas. However, after establishment, it does not necessarily follow that areas surrounding sites of initial establishment will be conducive to rapid population growth and expansion of the invasive range. That is, patterns of invasion richness are the result of both establishment and spread and therefore patterns of invasion richness may not exactly mirror those of establishment locations.

Geographic variation in establishment and invasion richness may be driven, in part, by frequent human-aided movement of pests into specific regions (Brockerhoff, Kimberley, Liebhold, Haack, & Cavey, 2014), forest structure including host availability and/or apparency (Guo, Fei, Potter, Liebhold, & Wen, 2019; Liebhold et al., 2013), and climate (Ward & Masters, 2007). Among other factors, establishment and invasion richness might also be influenced by global regions of origin and/or guilds of invaders. For example, rates of establishment and spread may be greatest when pests are moved between regions with similar climates (Roura-Pascual et al., 2011; Venette, 2017) or more wood-borers may arrive in areas with high imports of wood packaging material (Brockerhoff, Bain, Kimberley, & Knížek, 2006; Haack, 2006; Rassati, Faccoli, Toffolo, Battisti, & Marini, 2015). Following establishment, spread may be guild dependent, for example, if firewood, a major pathway for wood-boring insects (Koch, Yemshanov, Magarey, & Smith, 2012), is moved with different frequencies between two regions than live plant material, a major pathway for foliage- and sap-feeding insects (Liebhold et al., 2012). It is unclear if either global region of origin or guild mediate patterns in establishment locations or invasion richness.

Here, we quantify spatial patterns in discovery points and invasion richness of non-native forest pests using spatial point pattern and hotspot analyses, respectively. Application of spatial point pattern analyses to ecological data has increased over the previous ~20 years and been frequently used to quantify spatial aggregation patterns (e.g., compete spatial randomness) in univariate data (Velázquez, Martínez, Getzin, Moloney, & Wiegand, 2016). Point pattern analyses may also be used to quantify the influence of spatial heterogeneity (e.g., habitat features) on point patterns (Dodd, McCarthy, Ainsworth, & Burgman, 2016; Li et al., 2017) and conduct marked point pattern analyses, which enable the inclusion of trait information (Velázquez et al., 2016). To that end, we analysed changes in first discovery points by time period of introduction, origin, and guild. For analyses of invasion richness, we identified richness hotspots by estimating local Getis–Ord statistics (Getis & Ord, 1992) at the county level. Relationships among first discovery locations, invasion richness, and richness hotspots were also investigated. Our intention was to provide insight on underlying drivers of macroscale patterns of invasion by non-native forest pests. We anticipate that our findings will assist management agencies in targeting areas for increased monitoring and mitigation efforts.

2 | MATERIALS AND METHODS

2.1 | Data collection and processing

The locations of first detection, or discovery points, and county-level occurrence for 101 major non-native pests (n = 84 insects, 17 pathogens) of trees were compiled for the contiguous USA. Data were originally collected for the Alien Forest Pest Explorer database. Briefly, locations (latitude, longitude) of discovery and occurrence at the county level were compiled from primary literature articles, surveys, and federal and state governmental reports. A detailed description of the database was provided in Liebhold et al., (2013), which focused on mapping invasion richness at the county level and identifying terms for propagule pressure and habitat invasibility that explained variation in invasion richness. Here, we conducted analyses to predict spatial patterns in discovery locations and quantitatively identify invasion hotspots (see below). For each pest, we obtained the year of first discovery, global region of origin or simply "origin" (Asian Palaearctic, Australasia, European plus Asian Palaearctic, European Palaearctic, or Neotropic Mexico/Central/South America; based on a pest's native range and henceforth referred to as Asia, Australasia, Eurasia, Europe and Mexico/Central America/South America respectively), and guild (bark/wood-borer, foliage-feeder, sap-feeder, pathogen). Pests were discovered between 1794 and 2004. Most were introduced from Asia (33) and Eurasia (33), followed by Europe (25), Australasia (8) and Mexico/Central America/South America (2). Of the total pests, 23 were bark/wood-borers, 34 were foliage-feeders, 27 were sap-feeders and 17 were pathogens.

For analyses of discovery points, some pests were not included either due to lack of documentation or because points were only traceable to the state level. One pest, beech scale (*Cryptoccocus fagisuga* Lind.), was removed from analysis of discovery points because this species arrived in the USA via diffusive spread from Canada rather than as a point introduction. Some pests were assigned to county centroids and were retained for analyses. Ten pests (n = 4 insects, 6 pathogens) were discovered in two, isolated locations and were treated as independent data points. In total, 79 discovery points for 74 pests (n = 62 insects, 12 pathogens) across 62 US counties were available for analyses of discovery points (Figure 1).

Hotspot analyses of invasion richness focused on 101 pests across 3,109 counties and were current as of July 2018. First discovery locations were not available for all pests; hence, number of species between first detection point analyses and hotspot analyses differed. Two pests, soapberry borer (*Agrilus prionurus* Chevrolat) and oak wilt [*Bretziella fagacearum* (T. W. Bretz) J. Hunt], originating from Mexico/Central America/South America were not included in origin-dependent analyses. Summaries of pests analysed for discovery points (Supporting Information Appendix S1: Table S1.1) and hotspots (Supporting Information Appendix S1: Table S1.2) by origin × guild are available in Supporting Information Appendix S1. All data and geographic information system (GIS) layers used in analyses are available through the Purdue University Research Repository (PURR) (Ward, Fei, & Liebhold, 2019).

2.2 | First discovery points

We analysed the spatial intensity of discovery locations (points per km^2) using spatial point pattern analysis (Renner et al., 2015). Our spatial window of analysis was the border of the entire contiguous USA. All points were projected using Albers equal area projection. We then quantified Ripley's K function [$K(r)$; Ripley, 1976] for discovery points, which provides inference on spatial clustering of points within circles of increasing radii (i.e., at various spatial scales; Bivand, Pebesma, & Gómez-Rubio, 2013). The estimated $K(r)$ was transformed ($\sqrt{K(r)/\pi}-r$) and compared visually to $K(r)$ values simulated from a random distribution of 200 points. All point pattern analyses were conducted in R statistical software (R Core Team, 2018) via the "spatstat" package (Baddeley, Rubak, & Turner, 2015; Baddeley & Turner, 2005).

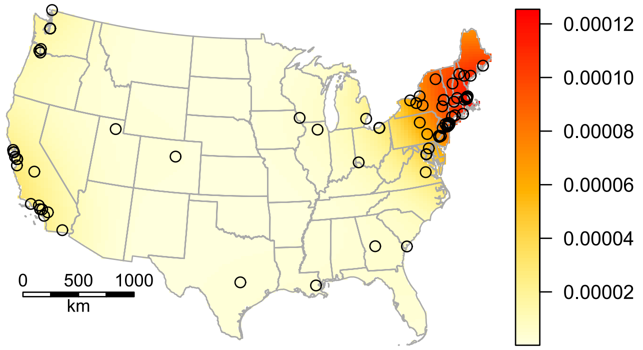


FIGURE 1 Intensity of discovery points (points per km^2) of non-native forest insects and pathogens discovered in the contiguous USA between 1794 and 2004. Colours and scale bar indicate a kernel smoother fit to observed first discovery locations, indicated by black circles. Map projection: Albers equal area

We then evaluated the explanatory power of invasion pathway variables for the log-transformed intensity of discovery locations using point process models. Predictors considered were population density in 1990 (converted to 10 km × 10 km raster; Falcone, 2016), coastal port density (National Geospatial-Intelligence Agency, 2017), road density (primary roads; US Census Bureau Department of Commerce, 2016), and first- and second-order terms for the west–east and south–north directions. Non-directional terms were converted to pixel-images for analysis (Baddeley & Turner, 2005). Note that our analyses predicted where pests were discovered, not necessarily where they first became established. The west–east and south–north terms were included as putative correlates for the arrival of pests in coastal areas by means not accounted for by the invasion pathway variables. For example, a positive correlation between west–east and intensity of first discovery points would indicate that there are statistically higher concentrations of points in the east versus west. Approximately 80,000 quadrature points were selected to approximate the integral in the log-likelihood function that is maximized when fitting point process models (Baddeley & Turner, 2005; Renner et al., 2015). Diagnostic plots of residuals suggested that substantial unexplained variation in both the west–east and south–north directions remained (Supporting Information Appendix S2).

We further analysed the location of discovery points in relation to time periods of discovery, origins, and guilds. To investigate temporal patterns in aggregation, the discovery point data were split into four groups using quartiles (Q1 = 1794–1907, Q2 = 1908–1927, Q3 = 1928–1991, Q4 = 1992–2004) for year of first discovery and Ripley's K was then estimated separately for each quartile. Following the approach of Bivand, Pebesma, et al. (2013), we also conducted pairwise comparisons of aggregation between time periods to determine, for example, if discovery points from time period i were more or less aggregated than those of time period j (graphical results of pairwise comparisons are provided in Supporting Information Appendix S3). We then conducted a marked point pattern analysis, which enabled each point to be assigned to a level of time period, by fitting a point process model with spatial covariates for the west–east direction, south–north direction and each direction's interaction with a term for time period (i.e., west–east × time period, south–north × time period; time period had four levels, Q1–Q4). Thus, we quantified (a) aggregation and (b) directional trends of points in space. Parallel analyses were conducted using origin and guild, each a categorical variable with four levels as described above, instead of time period. Trends were assessed visually by graphing intensity of discovery points as estimated via an isotropic Gaussian smoothing kernel fit via the density.ppp() function in R (Baddeley & Turner, 2005; Diggle, 1985). To determine robustness of full models, individual models for each level within a predictor were constructed by fitting terms for the west–east and south–north directions (e.g., assessing directional trends for pests introduced in Q1) and are provided in Supporting Information Appendix S4.

Finally, to determine if patterns associated with origin or guild changed with time, we fit two separate ANOVAs assessing the role of origin or guild in year of first discovery. When significant variation in discovery year was explained by a predictor (either guild or origin), we conducted Tukey's honest significant difference (HSD) tests using the "emmeans" package (Lenth, 2018) in R for pairwise comparisons.

2.3 | Current invasion hotspot patterns

Hotspot analyses compare attributes of spatial features, such as the invasion richness of a county and its neighbours, to the global pattern across all spatial features to identify those with attribute levels greater than would be expected due to random chance (Fei, 2010; Iannone et al., 2016; Patil & Taillie, 2004). Invasion hotspots were identified by quantifying local Getis–Ord (G_i^*) statistics (Getis & Ord, 1992) for each county in the data set. G_i^* is a local neighbourhood statistic that can account for invasion richness in neighbouring counties and enable one to detect spatial patterns that may not be accounted for when using global statistics (Ord & Getis, 1995). Thus, a county with low invasion richness could be identified as a hotspot if it is surrounded by counties with extremely low invasion richness values. Moreover, estimating G_i^* produces a Z-score, which can be used as a threshold value for identifying areas with high invasion richness, rather than a scale of integer values such as invasion richness counts. That is, invasion richness counts do not involve a statistical test to determine which areas have significantly higher richness.

A first-order spatial neighbourhood was constructed for calculating G_i^* statistics. Separate analyses were conducted for all pests combined, origins, and guilds. For origin and guild, we quantified G_i^* statistics both among (i.e., to identify counties with significantly more origins or guilds) and within (i.e., to identify counties with significantly more species belonging to a specific origin or guild) groupings. Calculating G_i^* statistics results in a Z-score that can be compared to a standard normal distribution to obtain a p-value. We defined a hotspot as any $Z \geq 4.16$ (i.e., $p < .05/3,109$ or $< .00002$), equivalent to a Bonferroni correction, to protect against inflated type I error rates from calculating 3,109 Z-values (one for each county).

2.4 | Current invasion hotspot patterns and first discovery locations

To quantify the effect of discovery locations on invasion richness, we first estimated the intensity of discovery points at county centroids from observed discovery point data using an isotropic Gaussian smoothing kernel fit using the density.ppp() function in R (Baddeley & Turner, 2005; Diggle, 1985) See Figure 1 for a representation of the smoothed surface. Estimated intensities were between 0.0000001 to 0.00011 pests per km^2. We then fit three spatial simultaneous autoregressive error (SAR) models. For the first two, we predicted invasion richness and hotspots, using estimated Z-values, as a function of estimated intensities of discovery points. For the third model, we regressed hotspot Z-values on invasion richness. Model residuals for each analysis were weighted by second-order spatial neighbourhoods to account for spatial autocorrelation, which was assessed by quantifying Moran's I. The SAR models were fit and Moran's I estimated using the "spdep" package in R (Bivand, Hauke, & Kossowski, 2013; Bivand & Piras, 2015). GIS analyses relied on the "geosphere" (Hijmans, 2017), "geostatsp" (Brown, 2015, 2018), "maptools" (Bivand & Lewin-Koh, 2017) and "rgdal" (Bivand, Keitt, & Rowlingson, 2018) packages in R (R Core Team, 2018).

3 | RESULTS

3.1 | First discovery points: Population density, ports, and roads

Discovery points were concentrated in the north-east and western coastal areas except for *c*. 10 points (*c*. 12%) distributed across the inland and southern USA (Figure 1). Owing to a total of 79 discoveries across the entire contiguous USA, the mean intensity was low (0.00001 points per km^2). Discoveries were highly aggregated in space at both local and continental scales (Figure 2a). In point process models, first- and second-order terms for west–east (west–east^2) were significantly, positively correlated with the intensity of discovery points, indicating that more pests initially invaded on both the east and west coasts (Table 1). Neither a first- nor second-order term for south–north was significant. After accounting for these directional trends in discovery points, the density of ports and roads, proxies for invasion pathway intensity (propagule pressure), were positively correlated with the intensity of discovery points (Table 1). Human population density was not significantly correlated with intensity of discovery points in our full model (Table 1), but was significantly, positively correlated when fit alone with the directional predictors (Supporting Information Appendix S5).

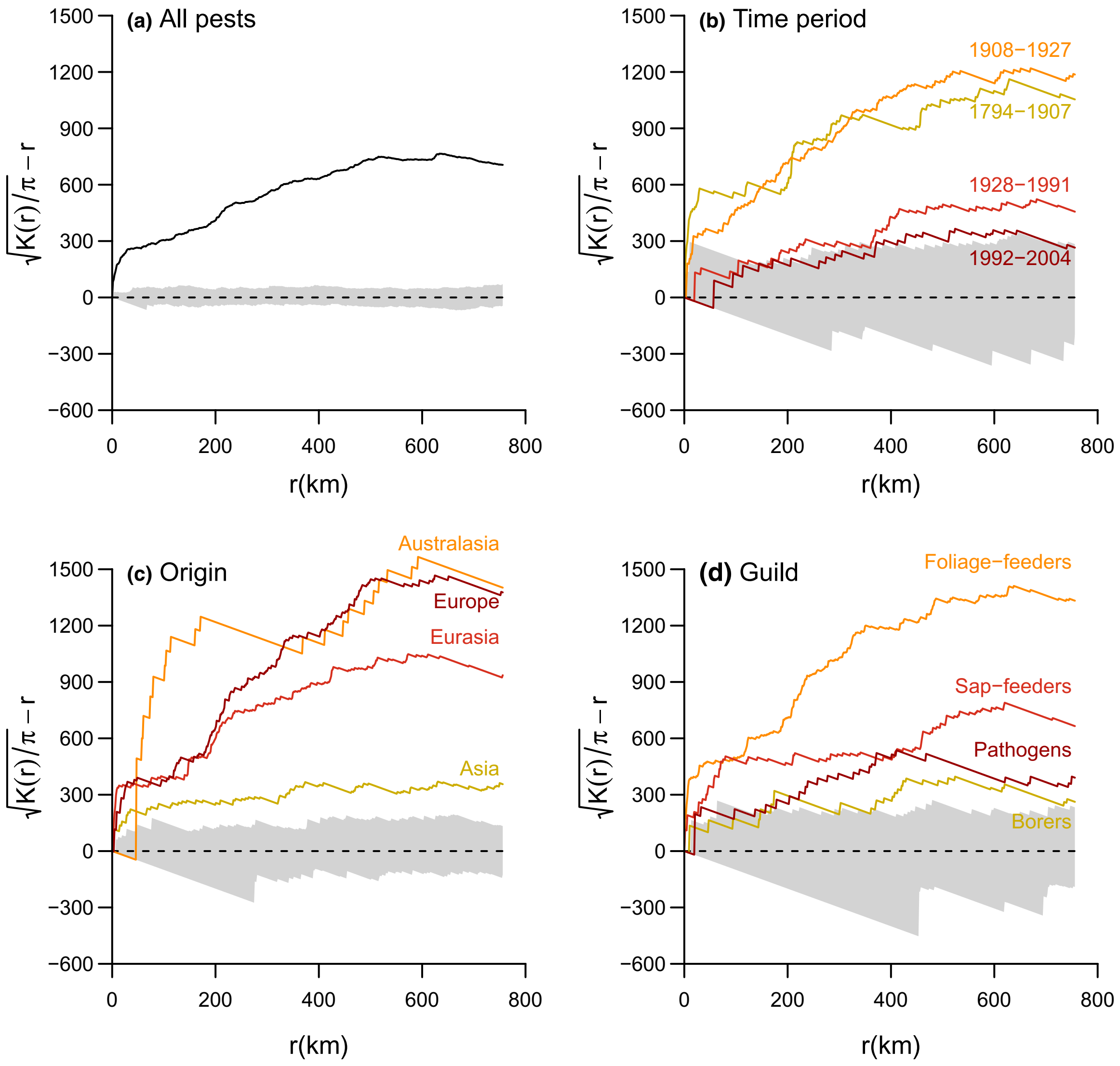


FIGURE 2 Transformed Ripley's *K* (*y* axis) for discovery points of non-native forest insects and pathogens discovered in the contiguous USA between 1794 and 2004 as a function of scale (radius of circles in km, *x* axis). Panels display discovery point patterns across (a) all pests, (b) time period of discovery, (c) origins or (d) guilds. Solid lines indicate observed, transformed *K*(*r*) at a radius *r* km from each discovery point. The dashed line provides an estimate of complete spatial randomness and the grey area represents 95% confidence limits for *K*(*r*) simulated from a theoretical, random distribution of discovery points. Lines above grey areas are significantly aggregated at the scale of analysis. For example, discoveries of all pests (panel a) are highly aggregated, regardless of scale

TABLE 1 Summary statistics from a spatial point process model evaluating the role of invasion pathway variables and terms for cardinal directions in intensity of first detection points, log(points per km^2), of non-native forest insects and pathogens discovered in the contiguous USA between 1794 and 2004. The terms west–east and south–north represent geographic coordinates in Albers projection (km). Model Akaike's information criterion (AIC): 1,571

Covariate	Estimate[a]	*SE*	|*Z*|[b]	*p*
Intercept	−14.12	0.39	36.39	< .0001
Population density	0.00006	0.00007	0.81	.29
Port density	0.37	0.15	2.57	.0149
Road density	0.00704	0.00081	8.68	< .0001
West–east	0.00041	0.00008	5.01	< .0001
West–east^2	10.2×10^{-7}	1.3×10^{-7}	8.00	< .0001
South–north	0.00009	0.00027	0.35	.38
South–north^2	-2.0×10^{-7}	3.5×10^{-7}	−0.58	.34

[a] Exponentiated coefficients for point process models indicate the factor by which density of discovery locations would increase per unit area with a one-unit increase in the density of a covariate. For example, holding all else equal, an increase in 1 port per km^2 was associated with a 1.4× [= exp(0.37)] increase in discovery points per km^2.

[b] *Z* statistics indicating whether coefficients estimated using spatial point process models are significantly different from 0.

TABLE 2 Spatial covariates of the intensity of first detection points, log(points per km^2), of non-native forest insects and pathogens discovered in the contiguous USA between 1794 and 2004. Trends were analysed using marked spatial point process models. Three separate analyses were conducted in which points were marked by time period of discovery (a), origin (b) or guild (c). The terms west–east and south–north represent geographic coordinates in Albers projection (km)

Covariate[a]	Estimate[b]	*SE*	|*Z*|[c]	*p*
a. Time period of discovery (AIC: 2,120)				
Intercept (Q1, 1974–1907)	−13.48	0.35	38.93	< .0001
Q2 (1908–1927)	−0.19	0.52	0.37	.37
Q3 (1928–1991)	0.51	0.43	1.19	.20
Q4 (1992–2004)	0.45	0.43	1.06	.23
West–east	0.00117	0.00025	4.76	< .0001
South–north	0.00110	0.00041	2.66	.0116
Q2 × west–east	0.00022	0.00037	0.60	.33
Q3 × west–east	−0.00076	0.00031	2.45	.0200
Q4 × west–east	−0.00113	0.00034	3.35	.0014
Q2 × south–north	0.00001	0.00059	0.02	.40
Q3 × south–north	−0.00001	0.00057	0.02	.40
Q4 × south–north	−0.00116	0.00056	2.05	.0484
b. Origin (AIC: 1,994)				
Intercept (Asia)	−12.62	0.21	61.29	< .0001
Australasia	−29.11	9.12	3.19	.0024
Eurasia	−0.64	0.37	1.73	.09
Europe	−2.08	0.66	3.15	.0028
West–east	0.00053	0.00018	2.99	.0046
South–north	0.00051	0.00031	1.63	.11
Australasia × west–east	−0.01497	0.00419	3.57	.0007
Eurasia × west–east	0.00044	0.00026	1.68	.10
Europe × west–east	0.00147	0.00046	3.20	.0024
Australasia × south–north	−0.00945	0.00288	3.28	.0018
Eurasia × south–north	0.00106	0.00051	2.08	.0463
Europe × south–north	0.00082	0.00060	1.36	.16
c. Guild (AIC: 2,089)				
Intercept (foliage-feeders)	−15.05	0.78	19.39	< .0001
Borers	2.00	0.82	2.45	.0198
Pathogens	1.50	0.86	1.75	.09
Sap-feeders	2.18	0.81	2.70	.0104
West–east	0.00265	0.00052	5.06	< .0001
South–north	0.00065	0.00041	1.57	.12
Borers × west–east	−0.00230	0.00057	4.06	.0001
Pathogens × west–east	−0.00210	0.00057	3.71	.0004
Sap-feeders × west–east	−0.00262	0.00056	4.64	< .0001
Borers × south–north	−0.00005	0.00057	0.09	.40
Pathogens × south–north	0.00097	0.00066	1.46	.14
Sap-feeders × south–north	−0.00056	0.00054	1.03	.23

Abbreviation: AIC, Akaike's information criterion.

[a] Models predict the intensity of discovery points as a function of variables for west–east and south–north directions and a categorical predictor (each with four levels). For example, in model (a), the model reference level is Q1 (1974–1907), and thus the interaction of other levels of the variable time period with west–east and south–north are each compared to the slope coefficients of west–east and south–north associated with level Q1 (i.e., 0.00117 and 0.00110, respectively). In models (b) and (c), the reference levels for the variables origin and guild are Asia and foliage-feeders, respectively.

[b] Exponentiated coefficients for point process models indicate the factor by which density of discovery locations would increase per unit area with either a change between levels of a factor or a one-unit increase in the density of a covariate. For example, for model (a) and holding all else equal, a shift 500 km west between Q1 and Q4 was associated with 1.76× [= exp(0.00113 × 500 km)] increase in the number of discovery points per km^2.

[c] *Z* statistics indicating whether coefficients estimated using spatial point process models are significantly different from 0.

FIGURE 3 Discovery locations of non-native forest insects and pathogens discovered in the contiguous USA between 1794 and 2004 displayed by time period (a–d; quartiles of introduction year), world region of origin (e–h) and feeding guild (i–l). Models comparing changes in the distribution of points by time period (row 1 of figure), origin (row 2) and guild (row 3) are provided in Table 2. Changes in aggregation between groupings are presented in Figure 2. Map projection: Albers equal area

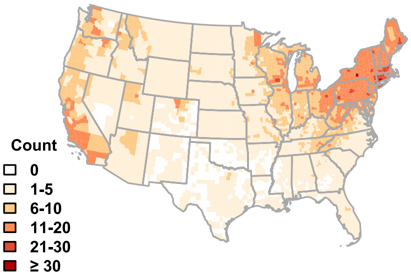
3.2 | First discovery points: Time period

When modelling the intensity of discovery points using marked point pattern analysis, we found that spatial patterns in discoveries varied among time periods. Pests discovered between 1794–1907 (Q1) and 1908–1927 (Q2) were significantly more aggregated than pests discovered between 1928–1991 (Q3) and 1992–2004 (Q4) (all $p < .01$; Figure 2b). There were no statistical differences between Q1 versus Q2 and Q3 versus Q4. When analysing how directional trends and time period of introduction (Q1–Q4) jointly influence discovery point intensity, there was a statistically significant interaction between both directional predictors and time (Table 2a, west–east × time period and south–north × time period). Pests discovered between 1794–1927 (Q1–Q2) were more likely to be discovered in eastern and northern regions of the USA (Table 2a, Figure 3a,b). Pests discovered from 1928–1991 (Q3) were more likely to be discovered farther west than pests from Q1 (Table 2a, Figure 3c). Pests discovered from 1992–2004 (Q4) were more likely to be discovered farther south and west than pests from Q1 (Table 2a, Figure 3d). Individual fits by time period confirmed that discoveries were more likely to occur father west and south as time progressed (Supporting Information Appendix S4: Table S4.1).

3.3 | First discovery points: Origin

Marked point pattern analyses demonstrated that, in addition to changes with time period, spatial patterns of discovery points were mediated by pests' global region of origin. Within an origin, all pests were aggregated in space (e.g., pests from Asia were likely to be discovered near other pests from Asia), although discovery points of pests from Australasia, Eurasia and Europe were more aggregated than those from Asia (Figure 2c). There were no differences in aggregation among discovery points of pests from Australasia, Eurasia and Europe. Pests from Asia were more likely to be discovered in the east versus the west (Table 2b, Figure 3e). Pests originating in Australasia were more likely to be discovered in the south-western USA than those from Asia (Table 2b,

(a) All pest counts



(b) All pest hotspots

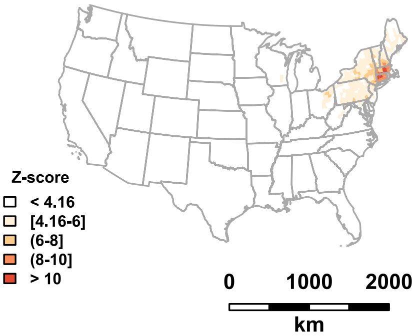


FIGURE 4 County-level (a) invasion richness and (b) hotspots for non-native forest insects and pathogens as of 2018 in the contiguous USA. Hotspot analyses enable comparisons of invasion richness of a county and its neighbours to the global richness patterns across all counties to identify counties with richness levels greater than would be expected due to random chance. Invasion hotspots were identified by quantifying local Getis–Ord (G_i^*) statistics, which produces a *Z*-score. Counties with *Z*-scores ≥ 4.16 were considered invasion hotspots. Map projection: Albers equal area

Figure 3f), whereas pests from Eurasia and Europe were typically discovered in the north-eastern USA, similarly to pests from Asia (Table 2b, Figure 3g,h). Individual fits by origin confirmed that pests from Asia, Eurasia and Europe were generally discovered in the east whereas pests from Australasia were discovered in the south-west (Supporting Information Appendix S4: Table S4.2).

3.4 | First discovery points: Guild

We also found that spatial patterns in discovery points differed among guilds. Discoveries of foliage-feeders were significantly more aggregated than borers, sap-feeders and pathogens (all $p < .01$; Figure 2d). There were no other differences detected in aggregation among guilds (all $p > .05$). Foliage-feeders were more likely to be discovered in the north-eastern USA (Figure 3i), whereas borers (Figure 3j), sap-feeders (Figure 3k) and pathogens (Figure 3l) were more likely to be discovered farther west than foliage-feeders (Table 2c). Higher densities of discovery points of pathogens were observed at higher latitudes, although this trend was not statistically significant (Table 2c). Individual fits by guild confirmed conclusions from full models, except that the positive trend of discoveries of pathogens in the *y*-direction was statistically significant in the model evaluating pathogens alone (Supporting Information Appendix S4: Table S4.3).

3.5 | First discovery points: Origin and guild by time period

Year of first discovery did not vary with region of origin ($F_{4,74} = 2.10$, $p = .09$). Pests from Australasia were the most recently discovered group on average, with a mean discovery year of 1973 (±18 years *SE*), followed by pests from Asia (1943 ± 8), Eurasia (1928 ± 11) and Europe (1923 ± 12). Year of first discovery varied significantly among guilds. The means for year of first discovery of borers and pathogens were 1981 (±8 years *SE*) and 1949 (± 9), respectively, and did not differ significantly (Tukey's HSD, $t_{75} = 2.08$, $p = .17$). Foliage-feeders and sap-feeders were discovered, on average, in 1916 (± 9 *SE*) and 1918 (± 11), respectively, significantly earlier than borers (Tukey's HSD, all $t_{75} > 4.3$ and $p < .0004$). No differences were detected among foliage-feeders, sap-feeders and pathogens (Tukey's HSD, all $t_{75} < 2.29$ and $p > .10$).

3.6 | Current invasion hotspot patterns: All pests

Of the 3,109 counties comprising our analysis, 89% were invaded by at least one species (Figure 4a). The average number of species per county was 4.88 (± 0.09 *SE*; maximum = 36 species) and 6.3% of counties were identified as hotspots (i.e., $Z \geq 4.16$, $p < .00002$) as estimated by Getis–Ord (G_i^*) statistics (Figure 4b). Most hotspots were in the north-eastern USA except for one county in south-eastern Wisconsin (Figure 4b).

3.7 | Current invasion hotspot patterns: Origin

Species region of origin was associated with distinct geographic patterns. The average county had pests belonging to 1.62 (± 0.018 *SE*) origins. Pests from Asia were the most widespread and established in 80% of counties. Pests from Eurasia (50% of counties infested) were the second most widespread, followed by pests from Europe (28%) and Australasia (4%). Several counties in California and one county each in Idaho, Massachusetts and Montana were hotspots for the number of different origins represented (Figure 5a). That is, those counties had more origins represented than would be expected due to random chance. Hotspots based on origin were relatively limited in spatial extent for pests from Asia, Australasia, Eurasia and Europe, covering 7, 2, 6 and 5% of counties, respectively (Figure 5b–e). Hotspots for pests from Asia (Figure 5b) and Eurasia (Figure 5d) were concentrated in eastern counties, although two hotspots for Eurasian pests were identified in Washington state. Hotspots of pests from Australasia were concentrated in the south-west and Florida (Figure 5c), whereas hotspots for pests from Europe were located in several coastal and inland western counties, some counties in the upper Midwest and several north-eastern counties (Figure 5e).

FIGURE 5 County-level invasion hotspots for non-native forest insects and pathogens as of 2018 in the contiguous USA based on pest origin: (a) numbers of origins, (b) Asia, (c) Australasia, (d) Eurasia and (e) Europe. A hotspot is defined as any county where Getis–Ord (G_i^*) statistics (*Z*-scores) are ≥ 4.16. See Figure 4 and main text for description of G_i^*. Map projection: Albers equal area

3.8 | Current invasion hotspot patterns: Guild

Counts and distributions of guilds exhibited considerable geographic variation. The average county contained 2.22 (0.023 ± *SE*) guilds. Pathogens were the most widespread and were detected in 76% of counties, followed by foliage-feeders (64% of counties), borers (49%) and sap-feeders (34%). Hotspots for numbers of different guilds represented occurred in few counties (< 1%) and were concentrated in the north-east (Figure 6a). Hotspots for borers, foliage-feeders, sap-feeders and pathogens were limited in their spatial extent, covering 4.7, 5.2, 4.6 and 7.1% of counties, respectively (Figure 6b-e). Despite hotspots for borers (Figure 6b) and sap-feeders (Figure 6d) being the least geographically widespread, hotspots for both guilds were identified in the north-east and south-west. Additional hotspots for borers were found in Michigan and Wisconsin, with one hotspot in north-western Utah. Several counties throughout California were identified as hotspots for sap-feeders. Hotspots of foliage-feeders (Figure 6c) and pathogens (Figure 6e) were distributed similarly and concentrated in the north-east and some Midwestern states.

3.9 | Current invasion hotspot patterns and first discovery locations

Both county-level invasion richness (Figure 7a) and hotspot *Z*-values (Figure 7b) were positively correlated with estimated intensities of first discovery locations. That is, invasion richness was higher in counties located in areas with higher densities of first discovery points. Similarly, hotspot *Z*-values were significantly, positively correlated with invasion richness (Figure 7c). The simultaneous autoregressive error models used to regress invasion richness and hotspot *Z*-values on estimated intensities of discovery points sufficiently accounted for spatial autocorrelation (both

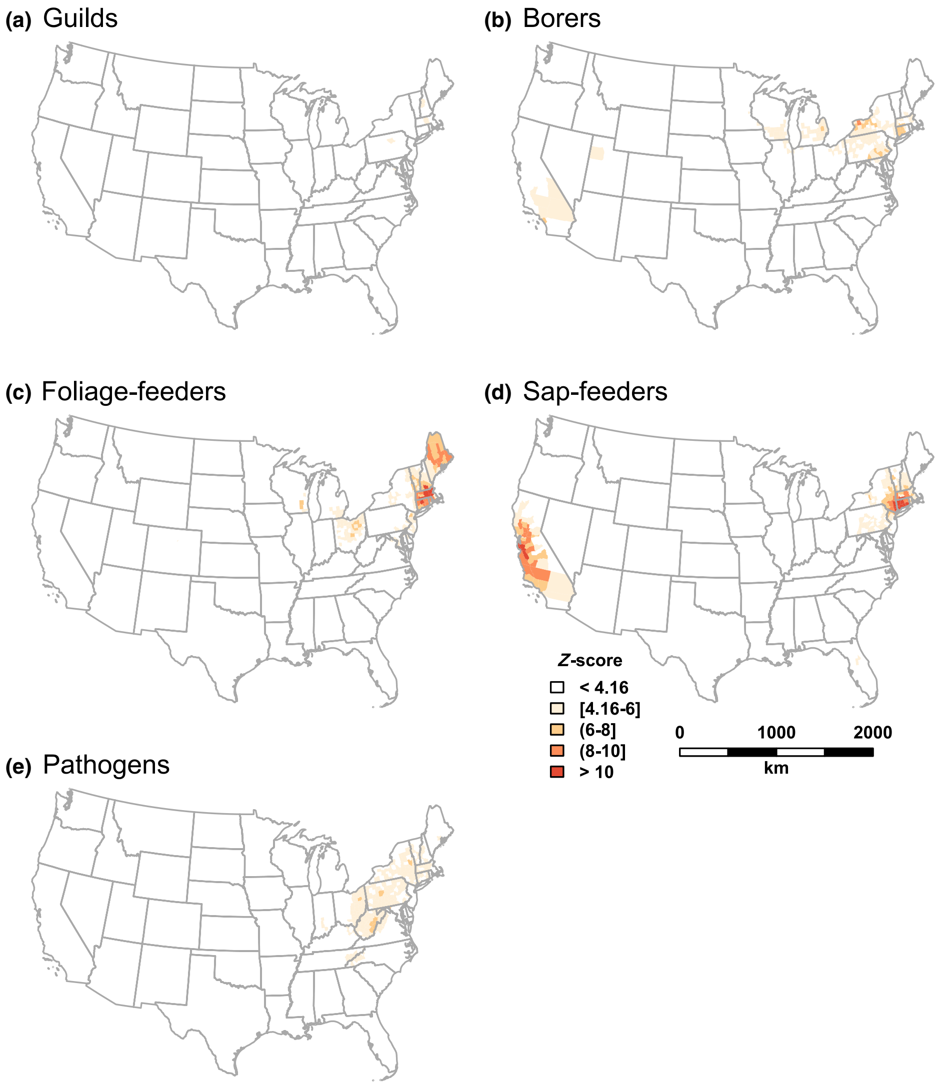


FIGURE 6 County-level invasion hotspots for non-native forest insects and pathogens as of 2018 in the contiguous USA based on pest guild: (a) numbers of guilds, (b) bark/wood-borers, (c) foliage-feeders, (d) sap-feeders and (e) pathogens. A hotspot is defined as any county where Getis–Ord (G_i^*) statistics (*Z*-scores) are ≥ 4.16. See Figure 4 and main text for description of G_i^*. Map projection: Albers equal area

Moran's $I < -.10$, $p = .99$). There remained some spatial autocorrelation in the model regressing hotspot *Z*-values on invasion richness (Moran's $I = .02$, $p < .05$).

4 | DISCUSSION

Our finding that discovery locations of forest pests are associated with human activity provides quantitative support for the role humans have in facilitating invasions. Movement of non-native species by humans has long been recognized (Hulme, 2009); however, we found that proxies for human activity, such as density of ports and roads, were more correlated with the intensity of discovery points than human population density itself (Table 1). Such findings may be indicative of frequent pest arrival in cargo imports (Aukema et al., 2010; Work, McCullough, Cavey, & Komsa, 2005). The final destination of contaminated cargo is not necessarily near the port of entry (Rassati et al., 2015) and areas with high densities of roads may contain many final destinations for cargo. The predictive ability of human population density may have been improved by considering population densities at earlier time periods (e.g., prior to the 1920s), given the relatively wide temporal window of our first discovery point data (1794–2004). Human population density, ports, and roads are also correlated in space, which may have masked the predictive power of population density (Supporting Information Appendix S5). Nonetheless, there remained unexplained variation in locations of initial establishment, as indicated by the strong association of discovery points with coastal regions after accounting for the densities of ports, roads and humans (Table 1), which may be attributable to habitat invasibility (e.g., tree diversity) (Guo et al., 2019; Liebhold et al., 2013).

The spatial distribution of discovery points differed between time periods and was dependent on pest origin and feeding guild,

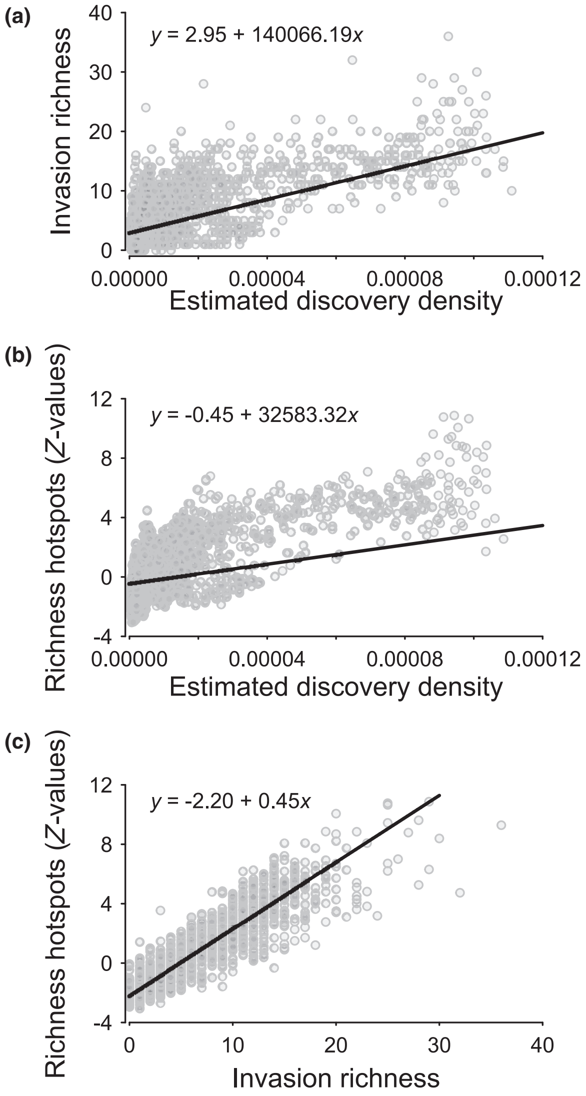


FIGURE 7 (a) Number of non-native pests per county as of 2018 in the contiguous USA (*y* axis; invasion richness) as a function of kernel estimated discovery points per km^2 at county centroids (estimated discovery density, *x* axis). The kernel smoother was fit to observed first discovery locations for non-native forest pests in the contiguous USA (1794–2004) and estimated discovery density for each county was obtained from that interpolated surface. Intercept (± 0.22 *SE*, $Z = 13.46$, $p < .0001$) and slope (± 7,816.57 *SE*, $Z = 17.92$, $p < .0001$) of fit line significantly differ from 0. (b) *Z*-values from hotspot analyses of invasion richness (richness hotspots, *y* axis) as a function of estimated discovery density at the county level. Intercept (± 0.14 *SE*, $Z = -3.18$, $p = .0015$) and slope (± 5,773.40 *SE*, $Z = 5.64$, $p < .0001$) of fit line significantly differ from 0. (c) Richness hotspots as a function of invasion richness. Intercept (± 0.02 *SE*, $Z = -132.48$, $p < .0001$) and slope (± 0.002 *SE*, $Z = 182.05$, $p < .0001$) of fit line significantly differ from 0.

likely reflecting changes in the intensity of invasion pathways, prevention/management efforts at ports of entry, or composition/volume of imports. For example, the historically dominant invasion pathway for foliage-feeders is the movement of live plants (Liebhold et al., 2012). Prior to 1918, imports of plants to the USA were largely unregulated but subsequent implementation of quarantine practices greatly diminished accidental introductions of insects on commercial plant imports (Liebhold & Griffin, 2016). We found that discoveries of foliage-feeders occurred the earliest on average (1916) and were concentrated in the north-eastern USA. Thus, the concentration of human populations in the north-east in the early 1900s coupled with unregulated importation of live plants likely drove the high aggregation of discovery points for foliage-feeders (Figure 2d). It follows that increased population density in the western USA would increase propagule pressure in the west and spread the risk of non-native pest establishment across a larger area, thus decreasing aggregation; indeed, we observed a decrease in aggregation through time (Figure 2b). Patterns of borer discovery also suggest that intensity of invasion pathways change with time. The average introduction year for borers was 1981, which may reflect temporal changes in their dominant invasion pathway, solid wood packaging material (Brockerhoff et al., 2006; Brockerhoff & Liebhold, 2017). Imports to the USA have risen dramatically over the last 100 years and widespread adoption of containerized cargo has led to increased movement of wood packaging and associated increases in borer invasions (Aukema et al., 2010).

We note that patterns in discovery points may be a function of sampling bias, with more pests discovered in areas of human activity due to survey efforts. However, invaders often arrive via pathways such that they typically establish in populated areas (Colunga-Garcia, Haack, & Adelaja, 2009; Paap, Burgess, & Wingfield, 2017) and thus first establishments in rural areas are generally low. Conspicuousness of impacts may also be an important determinant of first discovery point patterns. For example, there may be shorter time-lags between establishment and detection for pests with immediately visible impacts when at low densities. Variability in detection and/or imperfect detection may be able to be accounted for using occupancy models (Dorazio, 2014; MacKenzie et al., 2017). However, data on impact detectability, particularly when at low densities as is observed immediately following introduction, were not available and thus not accounted for in our analyses.

Hotspot analyses using all pest species indicated that hotspots were concentrated in the north-eastern USA, corroborating findings by Liebhold et al., (2013), but striking differences emerged when viewing hotspots by pest origin and guild. Hotspot patterns could be driven in part by the origin × guild composition of invasive forest pests. Hotspots of Australasian pests (Figure 5c) and sap-feeders (Figure 6d) were present in California and Florida, and 4/8 pests from Australasia were sap-feeders (only 4/27 sap-feeders were from Australasia; Supporting Information Appendix S1). Thus, the number of species per guild arriving from a place of origin could have contributed to some of the patterns in both first discovery points and hotspots observed here.

Invasion pathways begetting higher rates of establishment per unit area may, in part, drive subsequent patterns in invasion richness. That is, numbers of invasive forest pest species establishing in an area appeared to be associated with pest accumulation (Figure 7a) and invasion richness hotspots (Figure 7b) in surrounding areas. Quantification of spatio-temporal import trends may provide further insights, for example, if certain regions and time periods are associated with guild-dependent invasion pathways and associated establishments. We caution that our hotspot results may be scale-dependent; analysing data at the county level was ideal, however, given that (a) these data were recorded and quarantines are often imposed (e.g., emerald ash borer *Agrilus planipennisi* Fairmaire) at the county level and (b) hotspot analyses at the state level may have been limited by too few data points (i.e., 3,000 + counties versus 48 states).

Future analyses encompassing more discovery points, including those of pests of agricultural, rangeland and/or other ecosystems, may exhibit different patterns and/or provide insight into the behaviour of different invasion pathways. Patterns described here may not reflect the patterns of all non-native forest insects and pathogens, as our data are limited to tree insects and pathogens having some detectable impacts. Further analyses are also needed to examine the role of biotic resistance, the ecological characteristics of a community that decrease invasibility, in patterns of first discovery locations. Investigations of how diversity and structure of urban and rural forests affect pest establishment might help managers promote more pest-resistant landscapes (Jactel et al., 2009; Raupp, Cumming, & Raupp, 2006; Santamour, 1990). Nonetheless, our findings highlight the central role humans play in the movement and establishment of non-native forest pests and suggest continued monitoring near ports and highly populated areas to maximize early detection of new invaders.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

S.W. conceptualized the article, conducted analyses and wrote the initial draft. A.L. and S.F. assembled data and provided substantial input on analyses and writing.

DATA AVAILABILITY STATEMENT

All data and GIS layers used in analyses are available through the Purdue University Research Repository (PURR; https://doi.org/10.4231/7YT5-ET33).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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