



A highly aggregated geographical distribution of forest pest invasions in the USA

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ABSTRACT

Aim Geographical variation in numbers of established non-native species provides clues to the underlying processes driving biological invasions. Specifically, this variation reflects landscape characteristics that drive non-native species arrival, establishment and spread. Here, we investigate spatial variation in damaging non-native forest insect and pathogen species to draw inferences about the dominant processes influencing their arrival, establishment and spread.

Location The continental USA, including Alaska (Hawaii not included).

Methods We assembled the current geographical ranges (county-level) of 79 species of damaging non-indigenous forest insect and pathogen species currently established in the continental USA. We explored statistical associations of numbers of species per county with habitat characteristics associated with propagule pressure and with variables reflecting habitat invasibility. We also analysed relationships between the geographical area occupied by each pest species and the time since introduction and habitat characteristics.

Results The geographical pattern of non-native forest pest species richness is highly focused, with vastly more species in the north-eastern USA. Geographical variation in species richness is associated with habitat factors related to both propagule pressure and invasibility. Ranges of the non-native species are related to historical spread; range areas are strongly correlated with time since establishment. The average (all species) radial rate of range expansion is 5.2 km yr⁻¹, and surprisingly, this rate did not differ among foliage feeders, sap-feeders, wood borers and plant pathogens.

Main conclusions Forest pest species are much more concentrated in the north-eastern region of the USA compared with other parts of the country. This pattern most likely reflects the combined effects of propagule pressure (pest arrival), habitat invasibility (pest establishment) and invasion spread. The similarity in historical spread among different types of organisms indicates the importance of anthropogenic movement in spread.

Keywords

Biological invasions, forest insect and disease, habitat invasibility, pathway, propagule pressure, spread.

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INTRODUCTION

Increases in global trade and travel have intensified invasion pathways for a wide range of biota (Everett, 2000; Levine & D'Antonio, 2003). Despite efforts to exclude new introductions through quarantine measures, the number of

non-indigenous species established world-wide continues to increase (Ricciardi & MacIsaac, 2000; Hulme *et al.*, 2009a; Aukema *et al.*, 2010). The origin of some of the first North American invaders can be traced back to early colonial settlements (Crosby, 1986; Aukema *et al.*, 2010), but recent advances in global trade, such as the advent of containerized

cargo (Haack, 2006; Hulme, 2009b) and international movement of live plants (Liebhold *et al.*, 2012), are providing pathways for a new assemblage of potential invaders. Analysis of historical invasions and identification of changes in pathway strength help us understand trends in invasions (Everett, 2000; Aukema *et al.*, 2010).

In addition to temporal trends, spatial variation in invasion risk is of considerable importance in many systems. Some understanding of spatial variation has come by evaluating geographical variation in factors related to invasion risk. Such analyses have considered components of risk associated with habitat characteristics such as climate or host presence that affect the ability of invaders to establish (e.g. Whittier *et al.*, 2008; Venette *et al.*, 2010) or characteristics that affect propagule pressure, such as rates of cargo transport or ballast water discharge (e.g. Drake & Lodge, 2004; Koch *et al.*, 2011). However, these approaches to modelling risk have their limitations because the qualities of their predictions are entirely dependent on assumptions about the processes responsible for invasion risk. An alternative approach is the analysis of actual geographical distributions of numbers of invasions (e.g. Guo *et al.*, 2012). In one of the most comprehensive studies to date, Pyšek *et al.* (2010) found that numbers of non-native species of various taxa established in 55 European nations was primarily explained by economic and human demographic factors. Their analysis implicated propagule pressure as the dominant force driving geographical variation in numbers of invading species. They found less evidence to support geographical variation in habitat 'invasibility'. Such analyses are difficult, in part because geographical variation in numbers of invasions can result both from the arrival of species from distant locations and also from the range expansion of species already established in adjoining areas (Paini *et al.*, 2010). Disentangling these effects thus represents a challenge in the analysis of geographical variation in numbers of invaders.

Here, we address this problem by investigating geographical variation in numbers of non-native forest insect and pathogen species established across the continental USA, including Alaska. North American forests have been influenced, often intensely, by non-indigenous insects and forest pathogens for decades (Liebhold *et al.*, 1995; Niemela & Mattson, 1996; Lovett *et al.*, 2006). Non-native forest insects became established in the USA at a rate of 2.5 species per year estimated over the past century, while one damaging insect or pathogen species became established every 2 years (Aukema *et al.*, 2010). A notable example is provided by the fungus *Cryphonectria parasitica* (Murrill) Barr, the causal agent of chestnut blight. This pathogen nearly extirpated American chestnut, *Castanea dentata* (Marshall) Borkhausen, a species that at one time comprised 25% of the eastern hardwood forests, which extended over 81 million hectares (Anagnostakis, 1987). More recently, the emerald ash borer, *Agrilus planipennis* Fairmaire, which was inadvertently introduced from Asia to Detroit, Michigan, has killed tens of millions of North American ash (*Fraxinus* spp.) trees and its geographical

range continues to expand (Poland & McCullough, 2006). Ash species in North America have demonstrated little resistance to this phloem-feeding insect (Anulewicz *et al.*, 2008), generating concern that the entire genus may be functionally lost from forests across the continent.

We compiled a county-level database with the current distribution of non-indigenous forest insect and pathogen species in the continental USA (including Alaska). Unfortunately, the distributions of many non-native species are not well documented. Consequently, we limited our database to only truly invasive species, for example those known to be causing damage (Aukema *et al.*, 2010), because accurate distribution information is more widely available for these species. We then identified and evaluated habitat, economic and demographic characteristics to assess their ability to explain the geographical variation in numbers of invading forest insect and pathogen species. We further investigated the variability in current pest ranges and identified potential characteristics to explain the variability.

METHODS

Pest distribution data

Pest distributions were compiled for all non-indigenous forest insect and pathogen species known to cause economic impacts in the USA (Table S1 in Supporting Information). This list, originally published in Aukema *et al.* (2010), consists of 62 insect and 17 pathogen species. For insects, the list includes herbivorous species that feed on foliage, sap or as phloem- or wood-borers. Species such as predators, pollinators and ants were excluded. The earliest date of detection was recorded for each species. For seven species, the earliest detection records only referred to a decade, so the mid-point of the decade was used (e.g. a species detected in the 1960s was recorded as 1965). See Aukema *et al.* (2010) for a more detailed description of this list.

With a few exceptions (e.g. the gypsy moth, *Lymantria dispar*), there are no standardized surveys for non-native forest pests, and therefore, it was necessary to compile information about geographical ranges from a variety of sources. For example, the USDA Forest Service annually publishes a national 'Pest Conditions Report' (e.g. United States Department of Agriculture Forest Service (USDA FS), 2009) that provides distributional data for several non-native forest pest species. Another source of data were summaries of state-wide pest surveys conducted as part of the Cooperative Agricultural Pest Survey (United States Department of Agriculture Animal & Plant Health Inspection Service (USDA APHIS), 2005). From these various sources of pest distribution data, we recorded the current presence-absence of each pest species for individual USA counties. For two species, (*Profe-nusa thomsoni* (Konow) and *Cephalcia lariciphila* Wachtl), distributional records were only available at the state level, in which case all counties in selected states were designated as infested.

The county-level presence–absence data were compiled in a geographical information system using the ArcGIS software (ESRI, 2005). These geospatial data may be freely downloaded and interactively displayed at the ‘Alien Forest Pest Explorer’ web mapping site, maintained by the US Forest Service (<http://www.nrs.fs.fed.us/tools/afpe>).

Habitat data

We compiled a list of the primary tree species used as hosts by each pest, based on scientific literature, regulatory reports and university extension bulletins or related materials (Table S2). We then estimated the wood volume for the hosts in each US county for each pest species. These estimates were derived from forest inventory data collected by the USDA Forest Service Forest Inventory and Analysis (FIA) programme (Miles *et al.*, 2001). The FIA programme represents a network of permanent plots located throughout the forested regions of the USA designed to assess forest resources. While these data provide robust estimates of the composition of natural and planted forests, urban areas are excluded from FIA sampling. We used the FIA MapMaker online data query programme (Miles, 2001) to compile county-level estimates of volume for each species in the USA derived from thousands of inventory plots. Volumes of each host species were summed for each pest species by county. Maps of these host volume estimates are also available at the Alien Forest Pest Explorer Internet mapping site (<http://www.nrs.fs.fed.us/tools/afpe/maps>). These estimates of tree volume also allowed the determination of the presence–absence of each tree species by county and were used to tabulate species, genus and family richness for each county.

Along with counts of tree species, genus and family richness, we compiled additional county-level human demographic and economic data with the expectation that they may explain geographical variation in the number of pests per county. These variables included county area (km²), human population in 1900 (from US Census, <http://www.census.gov/population/cencounts/1900-90.txt>), human population in 2007 (from US Census, <http://www.census.gov/popest/data/intercensal/county/county2010.html>), per capita income (1999 in dollars, from US Census, http://quickfacts.census.gov/qfd/meta/long_INC910199.htm), distance (km) to the nearest port (we used ArcGIS to calculate distances from the ten USA ports with the largest yearly tonnage of imports in 2004 based on <http://www.aapa-ports.org/home.cfm>), total length (km) of all primary roads (calculated using ArcGIS based on the ArcGIS World Transportation reference layer (<http://www.esri.com/data/data-maps/data-and-maps-server>), and total forest land area (in km² extracted from the FIA MapMaker online data query programme).

Statistical analyses

The relationships between county-level non-native species richness and habitat features were explored using two

methods. The first approach involved the application of forward stepwise linear regression to model the number of invading pest species per county as a function of the host and other habitat variables described above. Ordinary linear regression model fitting such as this has limitations in its applicability to these data, however, because (1) there was a high degree of collinearity among the independent variables and (2) both dependent and independent variables were spatially autocorrelated, violating the implicit assumption of independence among samples.

To address the problem of collinearity, we applied principal components analysis to the habitat variables. First, we divided the variables into those most likely to affect propagule pressure (human population in 1900, human population in 2007, per capita income, distance to the nearest port and total length of all primary roads) and those most likely to affect habitat ‘invasibility’ (forest land area, number of host species, number of host genera and number of host families). For each of the two sets of variables, principal components analysis was used to derive two summary variables as the two primary axes. This yielded two propagule pressure variables and two invasibility variables for each county. The number of pest species per county was then regressed on these four independent variables using a simultaneous autoregressive spatial error (SAR_{err}) model (Kissling & Carl, 2008). The SAR_{err} analysis accounted for the spatial dependence in variables when testing for the significance of explanatory variables. Computations were performed using the SPDEP library (Bivand, 2006) of the R Language.

We also used the pest distribution data to investigate the determinants of pest range area. This was accomplished via application of a stepwise regression (0.15 significance level for model entry and 0.05 for staying in the model) of range area as a function of year of first detection of each pest, host density (tree volume density (m³ per km²) over the range), area of host range (km²) and number of known N. American host species (Tables S1, S2).

RESULTS

The geographical distribution of numbers of invasive forest pests shows a remarkably distinct pattern with a clear area of concentration in the north-eastern region (Fig. 1). At least 40 invasive forest pest species are established in most of NY, PA, MA and CT, followed by MI and VT, where 35 or more invasive pests are present. There are several potential explanations for this phenomenon, which we explored statistically.

Numbers of invasive forest pests per county were most highly correlated with the diversity of host trees (Table S3); the correlation was greatest with number of host genera, followed by number of families and then number of species. Tree species, genus and family richness were greatest in the eastern USA although forest area was greatest in the west (Fig. 2). These variables can be expected to be associated with the quality of the habitat (invasibility) for supporting

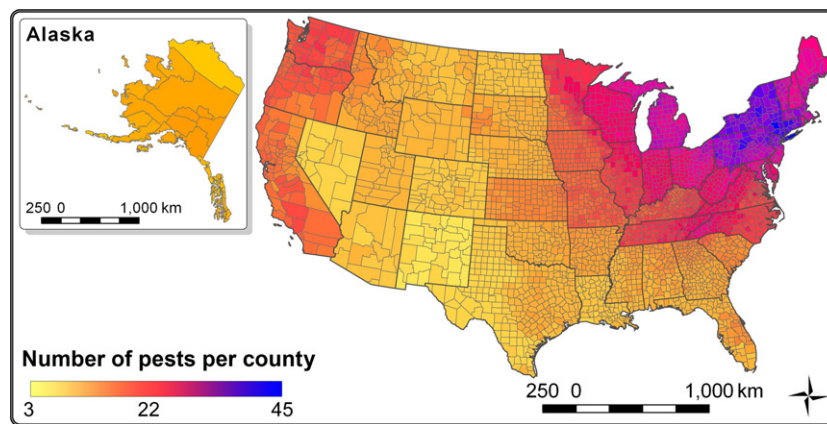


Figure 1 Numbers of damaging invasive forest pests per county.

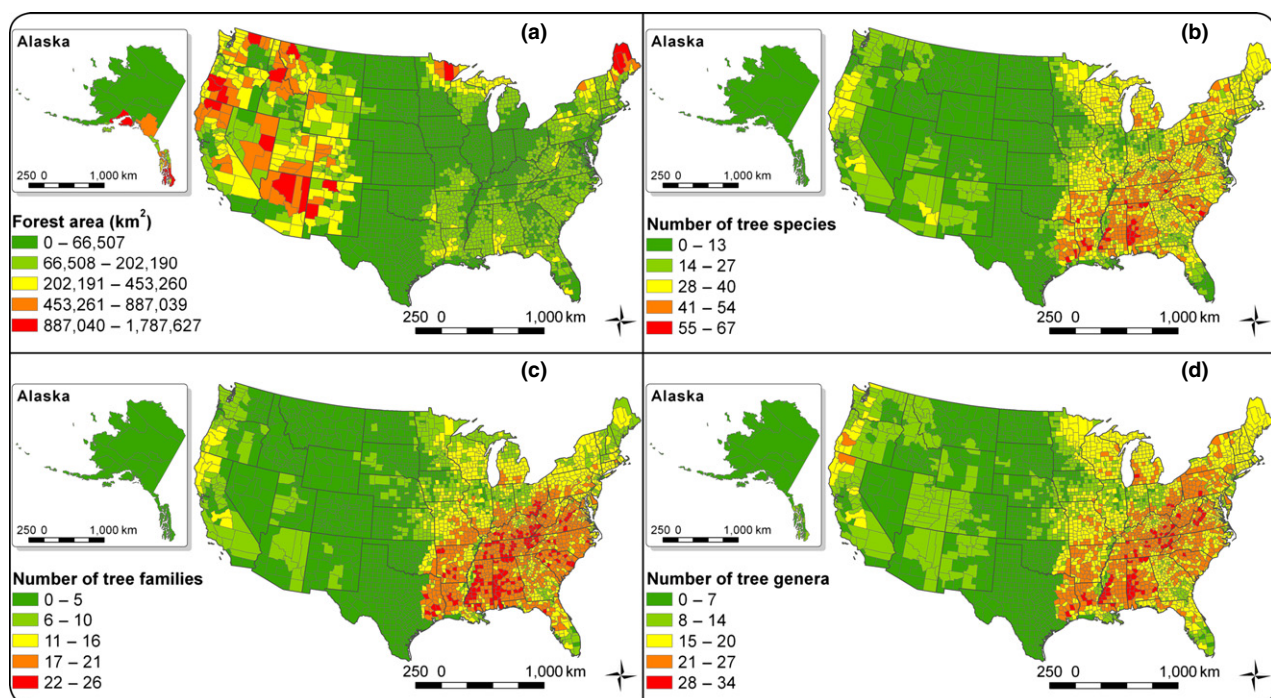


Figure 2 Variables associated with habitat invasibility measured at the county-level: (a) forested land area; (b) numbers of tree species detected in FIA surveys; (c) numbers of tree families detected in FIA surveys; (d) numbers of tree genera detected in FIA surveys.

new populations of invading pest species during the establishment phase.

Not surprisingly, number of host genera entered first into the stepwise regression on number of pest species (Table 1). However, it was followed by per capita income, a variable presumably reflective of propagule pressure (movement of organisms via trade and travel). Per capita income is generally greatest in the north-eastern region of the USA (Fig. 3).

There was generally a great deal of collinearity among the independent covariates (Table S3). In particular, numbers of host species, genera and families were highly correlated. To avoid this collinearity, we applied principal components

analysis to the four habitat variables reflecting invasibility and to the five variables associated with propagule pressure (Table S4). The first axis for propagule pressure was primarily associated with human population density in 2007 and road length, but the second axis was primarily associated with human population in 1900 and the distance to the nearest port. The first axis explained 45% of the total variance and the second axis explained 20%. For invasibility, the first axis was approximately equally determined by numbers of host species, genera and families, while axis two was primarily associated with the area of forested land per county. The first axis explained 74% of the total variance and the second axis explained 24%.

Analysis of the number of pests per county using the SAR_{err} model indicated that the first axis for propagule pressure (road length, road area and population in 2000) and the first axis for invasibility (number of host species, genera and families) were significantly associated with the total number of invasive species per county (Table 2). The second

Table 1 Results of stepwise regression on numbers of invasive forest pests per county

Variable	Entry into model	Estimate	Partial R^2	Pr ($> F$)
Intercept		5.29		< 0.0001
No. host genera	1	2.33	0.2057	< 0.0001
Per capita income	2	4.94 E-4	0.1073	< 0.0001
No. host families	3	-1.82	0.0861	< 0.0001
Forest area (km ²)	4	-4.21 E-4	0.0499	< 0.0001
Human population in 1900	5	1.82 E-5	0.0237	< 0.0001
No. host species	6	-0.279	0.0132	< 0.0001
Distance to port (km)	8	-7.21 E-7	0.0011	0.0084

axis for propagule pressure (distance from port, population in 1900) was marginally significant, but the second axis for invasibility (forestland area) was not significant in the model (Table 2).

The earliest record associated with the 79 invasive forest pests used in our analysis dates back to 1794, and 19 species were detected before 1900. The area currently occupied varies among these early invaders, ranging from 3732 to 8,540,557 km² (Table S1). Area occupied by recent invaders detected since 1990 ranged from 10,993 to 4,993,422 km². Results of stepwise regression on the current range area of each pest species showed that the year a pest was first detected explained the largest amount of the variation in range area ($df = 68$, $F = 33.16$, $Prob > F < 0.0001$). The parameter estimate for year of first detection was negative, reflecting the fact that more recently arrived species tend to have smaller ranges than long-established species. Neither host density, host range size nor number of host species remained in the stepwise model and therefore did not significantly explain variation in pest range area.

Regression of range radius ($\sqrt{\text{area}}/\pi$) on years since introduction yielded an estimate of mean radial range

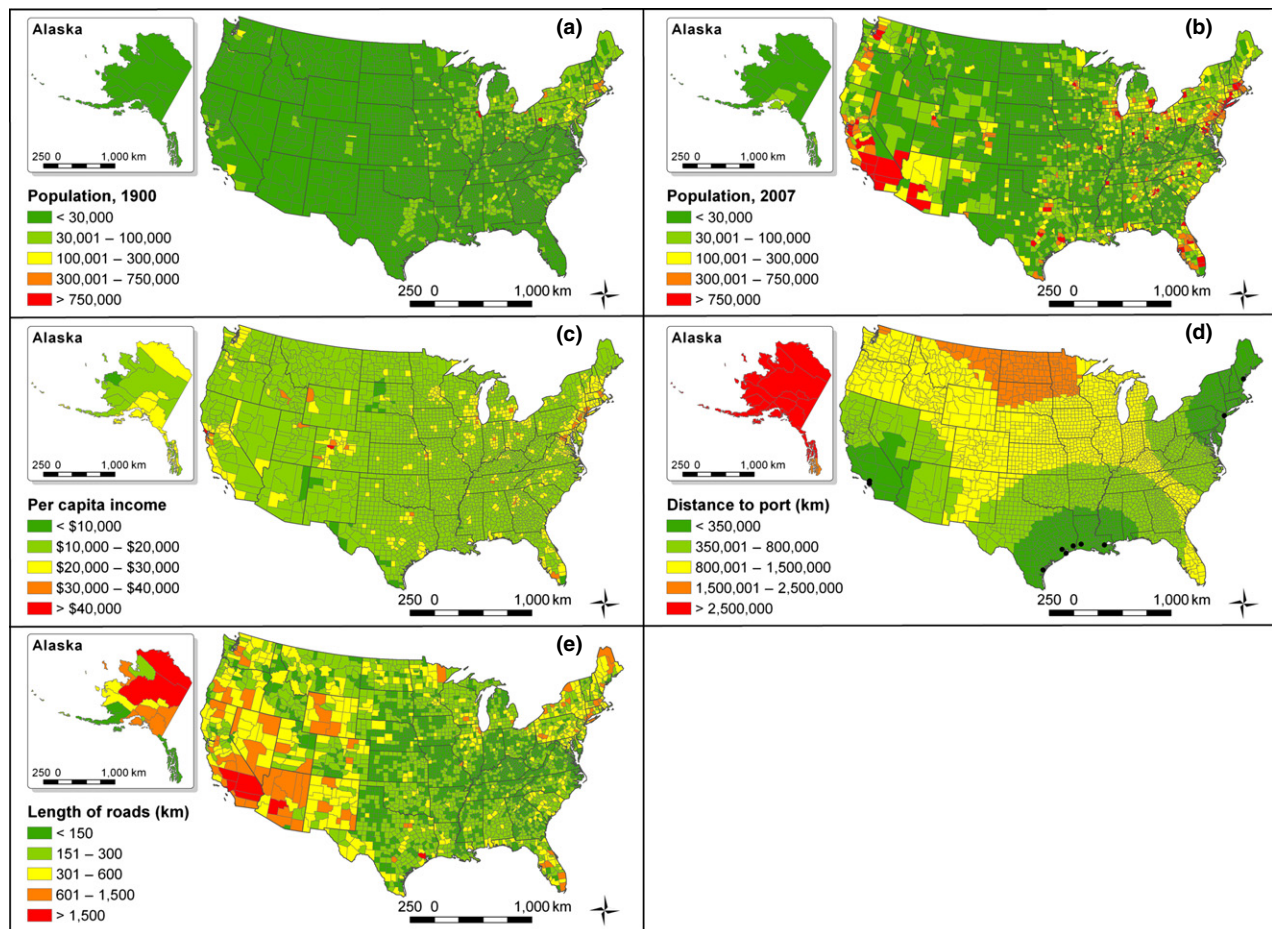


Figure 3 Variables associated with propagule pressure measured at the county-level: (a) human population size in 1900; (b) human population in 2007; (c) per capita income; (d) distance to nearest major port; (e) length of roads.

Table 2 Results from a simultaneous autoregressive error (SAR_{err}) model of numbers of pest species as a function of the two propagule axes and two invasibility axes.

	Estimate	Standard error	Partial R^2	z value	Pr ($> z $)
(a) Full model variable					
Intercept	14.2	28.8		0.492	0.622
Propagule axis 1	0.120	0.0208	0.0256	5.76	8.33 E-9
Propagule axis 2	-0.0937	0.0478	0.0830	-1.96	0.0498
Invasibility axis 1	0.471	0.0364	0.146	12.9	2.20 E-16
Invasibility axis 2	-0.0533	0.0533	0.00772	-1.00	0.317
(b) Reduced model variable					
Intercept	13.4	28.8		0.465	0.642
Propagule axis 1	0.118	0.0207	0.0206	5.68	1.32 E-8
Propagule axis 2	-0.103	0.0469	0.106	-2.19	0.0288
Invasibility axis 1	0.465	0.0359	0.143	12.9	2.20 E-16

expansion of 5.2 km yr⁻¹. An F test for lack-of-fit (Neter *et al.*, 1990) ($F = 0.84$, $df = 68$, $P = 0.0700$) failed to reject the null hypothesis that a linear regression model was statistically appropriate. The relationship between the year of detection and current range was generally similar for the pathogens and three guilds of insects (Fig. 4). Indeed, fitting a general linear model of range radius as a function of years since introduction indicated a lack of significant effect of guild on the intercept ($P = 0.667$) or on the slope ($P = 0.831$).

DISCUSSION

The striking variation in the geographical distribution of non-native forest pest species illustrated in Fig. 1 clearly demonstrates that the spatial distribution of invasive forest pests is not uniform or random. Instead, the distribution is highly focused, with a large number of species in the north-eastern region and then decreasing numbers radiating to the west and south. It is important to keep in mind that these numbers result from the culmination of all three phases of invasions: arrival, establishment and spread.

Propagule pressure is considered perhaps the most important determinant of non-native species establishment and areas where propagule pressure is greatest can be expected to have the highest rates of non-native species present (Lockwood *et al.*, 2005). The north-east is where industrialization historically began in the USA, and it is likely that pathways associated with industrialization (i.e. cargo imports) were particularly strong in this region. The fact that 75% of the invasive forest pests on our list were detected before 1940 (Table S1) is consistent with this pattern. Thus, it is not surprising that there are more alien pests established in the north-eastern USA (Fig. 1). Both principal components associated with propagule pressure explained a large fraction of the geographical variation in pest species richness (Table 2), again indicative of the importance of propagule pressure on arrival. Huang *et al.* (2012) reported that, in China, the locations of first detections of non-native species were most

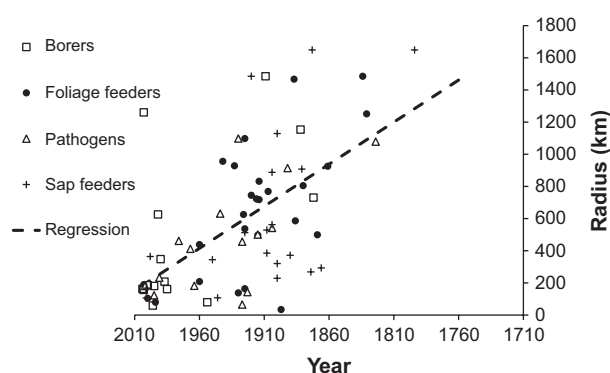


Figure 4 Pest range radius ($\sqrt{\text{area}}/\pi$) as a function of year of detection (note that detection year axis is reversed to more clearly illustrate the relationship between the area occupied by the pests and the number of years since establishment was detected).

numerous in coastal provinces, presumably reflecting historically high propagule pressure in those areas. Schlick-Steiner *et al.* (2008) and Pyšek *et al.* (2010) found economic and human demographic variables were associated with the geographical distribution of non-native organisms representing various taxa in Europe. They suggested that associations with these variables resulted from the impact of propagule pressure on establishment, as well as the impact of anthropogenic disturbance on invasibility.

One of the key elements affecting establishment of non-native forest insects and pathogens is the presence of suitable hosts. Our analysis confirmed that county-level diversity of host trees was positively associated with the number of established pest species (Tables 1 and 2, S3). The presence of a larger number of tree taxa allows for a broad range of herbivores to colonize an area (Southwood & Kennedy, 1983), and thus, host tree diversity increases invasibility for insects and pathogens. Taxonomic affinity between hosts in their native and exotic ranges can be expected to increase the probability of successful establishment by colonists

introduced into a new area (Niemela & Mattson, 1996). Broad-leaf (e.g. hardwood) tree species are abundant and diverse in north-eastern forests, and 65% of the insect and pathogen invaders on our list primarily colonize broad-leaf tree species. Establishment of both European and Asian forest insects and pathogens in North America has likely been facilitated by the similarity of the flora among these three continents (Mattson *et al.*, 2007). One limitation of our analysis is that we did not have access to exhaustive data quantifying the presence, and diversity of trees in urban settings where numerous invading species are believed to have first become established (Colunga-Garcia *et al.*, 2009).

The association that we observed between the distribution of invasive phytophagous insects and diversity of host trees and the general concentration of high alien species richness in the north-eastern USA are similar to patterns of diversity of introduced plant species (Bradley *et al.*, 2012) as well as the richness of native and exotic ambrosia beetles and bark beetles (some of which were included in our analysis) (Marini *et al.*, 2011). But it is not consistent with the geographical distribution of native bark beetles (Marini *et al.*, 2011). At large spatial scales, in particular, correlations between native and exotic species diversity have been found in a number of species groups (Stohlgren *et al.*, 1999; Sax, 2001; Fridley *et al.*, 2007; Lilleskov *et al.*, 2008; Chen *et al.*, 2010; Bartomeus *et al.*, 2011).

The eastern USA is characterized by a high density of wooded areas interspersed with urban and rural residential areas. This mixed land use combined with the high species diversity of eastern forests has likely promoted establishment of phytophagous insects and pathogens (Poland & McCullough, 2006). Thus, the concentration of established non-native species in the north-eastern USA (Fig. 1) likely reflects the combined effects, and perhaps synergistic interaction, between propagule pressure and invasibility.

Results from our statistical analyses generally confirm the hypotheses described above for explaining the focused distribution of non-native forest pest species. Both the 'naïve' tests (Table 1) and the more conservative tests that account for spatial autocorrelation (Table 2) indicate that both propagule pressure and habitat invasibility are positively associated with numbers of alien species.

Finally, it is important to acknowledge the importance of spread in shaping the distribution of pest species. Invasion spread is, by nature, highly contagious spatially; although long-distance 'jumps' sometime occur, invading populations mostly spread into adjoining areas (i.e. adjoining counties). This sort of process can be expected to accentuate any spatial contagion that may exist in either arrival or establishment rates and therefore also contributes to the highly focused pattern apparent in Fig. 1.

It is not surprising that the area occupied by an individual species is primarily determined by the number of years since its initial detection given the strong influence of spread on the current spatial distribution of these pests. Areas inhabited by species that have been present and spread for many years

are often extensive. However, it is surprising that the pattern of spread is not markedly different among the four different groups of invasive organisms. One would expect that relatively mobile species (e.g. pathogens with wind-borne spores) would exhibit much higher rates of historical spread than less mobile groups such as the scales and aphids that dominate the sap-feeding insects, but this has not been the case. A likely explanation for this unexpected result is the importance of long-range, inadvertent movement of pests by humans (e.g. Goss *et al.*, 2009; Haack *et al.*, 2010; Bigsby *et al.*, 2011).

Much in the same manner that industrialization and habitat invasibility promote pest arrival and establishment, these same habitat features can also promote spread. For example, there is ample evidence from the literature of the important human role in the spread of invading forest insects and pathogens (e.g. Gilbert *et al.*, 2004; Goss *et al.*, 2009). Similarly, tree diversity effects on invasibility may also promote spread. Thus, the statistical associations between habitat features influencing both propagule pressure and invasibility observed here (Tables 1 and 2) may have arisen during the arrival, establishment and spread phases of invasion, and it is not possible to completely separate effects among the various phases.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 List of non-indigenous forest pests known to damage forest trees in the USA.

Table S2 List of host tree species of non-indigenous forest pests with significant economic impacts in the USA.

Table S3 Correlation matrix among all dependent and independent county-level variables.

Table S4 Results of principal component analysis on habitat data.

BIOSKETCH

The work described here was performed as part of a working group, 'Economic impacts of non-native forest pests and pathogens in North America' at the National Center for Ecological Analysis and Synthesis. The overall objective of this group was to evaluate the economic impacts of forest insect and disease invasions in the United States.

Website: <http://www.nceas.ucsb.edu/projects/12031>.

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