EVALUATING THE FOREST PEST INVASION POTENTIAL OF TRADE-RELATED AND RECREATIONAL TRANSPORTATION PATHWAYS

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ABSTRACT

The successful establishment of invasive alien species in North America is strongly associated with global trade. Invasive insects and pathogens that affect plants are regularly introduced through international trade and domestic freight shipments, but few studies have directly quantified the invasion risks caused by commercial transportation at regional or larger scales. Similarly, despite much recent attention to the potential spread of forest pests with firewood transported by cars and other private or commercial vehicles, there has been little quantitative assessment of the invasion risks posed by this dispersal vector. In each case, a lack of empirical studies regarding human-mediated, long-distance spread of invasive organisms represents a key knowledge gap impeding realistic prediction of invasion patterns.

We present two studies in which we separately examined aspects of forest pest movement via commercial-trade-related and recreational transportation. Our first study estimated the likelihood of successful entry of alien forest insect species for >3,000 urban areas in the contiguous U.S. To develop these estimates, we first utilized data on historical merchandise imports and insect incursions to estimate an annual U.S. rate of alien insect species establishment with trade. Next, we used historical data on pest interceptions to calculate the proportion of all insects arriving at U.S. ports of entry that are associated with forest hosts. We then combined these results to estimate a nationwide establishment rate for alien forest insects. Finally, we used international and domestic commodity flow networks to allocate this nationwide rate to individual U.S. 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 are low (<0.005 new species/year), selected areas can expect the establishment of new alien forest insect species every 5-15 years.

Our second study analyzed forest insect spread with firewood and developed related dispersal functions for application in spatially explicit models. The primary data source was the U.S. National Recreation Reservation Service database, which records camper reservations at >2500 locations nationwide. We used "origin-destination" data for >7 million individual reservations (including visits from Canada) to construct an empirical dispersal kernel that estimates the likelihood of spreading an invasive organism as a function of geographic distance. We then fitted the data with various theoretical distributions. The data appear to be strongly leptokurtic and fairly well fit by the unbounded Johnson (SU) distribution (the lognormal distribution fit similarly). Most campers (~53%) traveled <100 km, but ~10% traveled >500 km (and as far as 5500 km). Additionally, we examined the impact of geographic region and proximity to major national parks and urban centers on the shape of the dispersal kernel, and found that mixture distributions may fit better in such circumstances.

These assessments represent initial steps toward improved depiction of human-assisted dispersal potential, and provide important functional inputs for quantitative models of invasion. Future work will focus on applications of our results in comprehensive, cross-border (U.S.-Canada) analyses of pest invasion risk and for specific probabilistic modeling efforts to trace the origins of established or anticipated infestations.

INTRODUCTION

Effective decision making for the management of a recently detected invasive species requires swift assessment of the species' expected behavior and pattern of expansion in its new environment. Unfortunately, it is challenging to quantify the risks presented by a new invader (e.g., of widespread establishment or substantial ecological impact), since they involve factors that interact across spatial and temporal scales, such as the population dynamics of the invading species, the environmental conditions in the invaded region(s), and the relative importance of various dispersal pathways (Barney and Whitlow 2008). In the absence of more definitive information sources, predictive models of the spatial spread of invasive species can provide useful guidance to decision makers who are tasked with devising management responses despite scarce resources to do so (Neubert and Parker 2004). However, reliable estimates regarding the rate and extent of long-distance dispersal events are necessary to model spread accurately (Hastings et al. 2005; Suarez, Holway, and Case 2001; Pitt, Worner, and Suarez 2009). Because long-distance dispersal events are rare, empirical data about them are difficult to obtain (Brown and Hovmøller 2002; Clark et al. 1998; Hastings et al. 2005; Higgins, Nathan, and Cain 2003; Hovestadt, Messner, and Poethke 2001), and in turn, estimates of their likelihood are typically uncertain (Nathan et al. 2003). This is especially true for invasive species, for which instances of long-distance dispersal are largely associated with human transport, particularly as related to global trade (Hastings et al. 2005).

Global trade and transportation are widely understood to be primary channels for the spread of invasive species into new geographic areas (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 this understanding, quantitative analyses of global trade and transportation pathways have been relatively limited in scope. A few studies have modeled the relationship between trade volume and number of invasive species, but only at broad spatial and/or taxonomic scales. For example, in a global analysis performed across multiple taxa, Westphal et al. (2008) found that a country's level of international trade (i.e., its volume of merchandise imports) serves as the best predictor of its number of invasive alien species. Similarly, Hlasny and Livingston (2008) asserted that agricultural import levels represent the best predictor of the number of insect species introduced into the U.S. Ultimately, to predict trade-related entries of invasive species at a finer scale (i.e., to provide better decision support) would require more detailed information about the quantity, origins, and destinations of various types of imports associated with the invaders (Hulme 2009; Hulme et al. 2008; Kenis et al. 2009).

Dispersal pathways related to trade are not the only concern. During the past several years, there has been growing alarm in North America about the potential for accidental (i.e., non-commercial) long-distance transport of invasive insects and pathogens in untreated firewood (Haack, Petrice, and Wiedenhoft 2010; Tobin et al. 2010). Both the U.S. and Canada have initiated national-scale public awareness campaigns about firewood (e.g., see Canadian Food Inspection Agency 2010; The Nature Conservancy 2011); currently, a majority of U.S. states impose some level of restrictions on firewood movement (The Nature Conservancy 2011). This attention to the firewood issue has primarily been driven by the high-profile invasion of eastern North America by the emerald ash borer (*Agrilus planipennis* Fairmaire), although the movement of infested firewood has also been implicated in the spread of other forest pests (Haack 2006; Kovacs et al. 2010; Petrice and Haack 2006). Previous studies indicate that firewood is regularly transported long distances (e.g., across state lines) for recreational or other non-trade-related purposes (Haack, Petrice, and Wiedenhoeft 2010; U.S. Department of Agriculture-Animal and Plant Health Inspection Service 2010). Notably, this long-distance dispersal potential of firewood has been incorporated into some spatial invasion models, especially for *A. planipennis* (BenDor and Metcalf 2006; BenDor et al. 2006; Harwood et al. 2010; Muirhead et al. 2006; Prasad et al. 2010), but in a simplified (i.e., non-empirical) fashion or based on very limited empirical data.

In both of the aforementioned cases, a lack of empirical data regarding human-mediated, long-distance spread of invasive species has represented a key obstacle to the realistic prediction of invasion patterns. Nevertheless, it is possible to maximize the value of the few available data by integrating them with general (i.e., not specifically invasion-oriented) data sets that depict trade and transportation patterns. By adopting certain analytical assumptions during the integration process, one may generate reasonable quantitative outputs for use in invasion prediction models. In this paper, we briefly summarize two studies – one concerned with commercial trade pathways, the other with recreational firewood transport – in which we performed quantitative, spatially referenced analyses regarding human-mediated dispersal of invasive species that affect forests. We also discuss the implications of our findings, as well as potential future directions in the analysis of human-mediated dispersal.

STUDY 1: ESTABLISHMENT POTENTIAL OF ALIEN FOREST INSECTS IN THE U.S.

In this study, we estimated annual rates of establishment across the U.S. for alien forest insect species. Our approach had two primary stages. First, we employed historical foreign trade and insect incursions data, as well as historical data on pest interceptions at U.S. ports of entry, to estimate an annual rate of alien forest insect species establishment for the entire U.S. Second, we used international and domestic commodity flow networks to estimate the alien forest insect establishment rate at >3,000 individual urban areas nationwide. We were motivated to look at urban forests because they are not only vulnerable to invasion by alien species, but also serve as gateways for subsequent invasions of natural forest ecosystems (Colunga-Garcia, Haack, and Adelaja 2009; Colunga-Garcia, Magarey, et al. 2010; U.S. Government Accountability Office 2006).

METHODS

We began the first stage of our analysis by estimating a total annual rate of alien insect species establishment (i.e., all insect species, regardless of ecological niche) for the contiguous U.S. To develop this estimate, we adapted the approach of Levine and D'Antonio (2003), who used species-accumulation models to estimate the number of new insect species that would be established in the U.S. between 2000 and 2020, based on historical import volumes and cumulative data on insect species incursions. Briefly, we re-parameterized their models (in particular, a log-linear species-area model) after updating their original input data in a few key ways. First, we extended their original historical record of insect species establishments (from Sailer 1983) with additional data from the North American Non-Indigenous Arthropods Database (NANIAD; see Kim and Wheeler 1991) . Second, we replaced their data regarding historical U.S. merchandise import volumes with the most recently revised numbers available (U.S. Department of Commerce 2009). Third, we replaced their original import projections through 2020 with new estimates (based on Nanto, Ilias, and Donnelly 2009) that accounted for the impact of the global economic downturn that began in 2007-2008.

Next, we used historical interception data to estimate the proportion of all insects arriving at U.S. ports of entry that are associated with forest hosts (i.e., tree species). Our primary data source was the PestID database, maintained by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (APHIS), which documents interceptions of alien organisms on materials arriving at U.S. ports of entry from other countries (Magarey, Colunga-Garcia, and Fieselmann 2009). Analyzing interceptions recorded between 1984 and 2008, we determined the proportion of forest insects by dividing the number of species records from eight wood-associated insect families (Haack 2006; U.S. Department of Agriculture-Animal and Plant Health Inspection Service 2006) by the total number of insect species records in the database. This proportion was subsequently multiplied by the species-accumulation model result to provide an estimate of the annual establishment rate of alien forest insect species in the U.S.

In the second stage of our analysis, we allocated this nationwide rate to all urban areas in the contiguous U.S. Our approach expanded on the methodology developed by Colunga-Garcia, Haack, and Adelaja (2009). To estimate the particular establishment rate for each urban area, we used data from the U.S. Freight Analysis Framework (FAF), a database that describes commodity flows among U.S. states, sub-state regions, and international trade regions (U.S. Federal Highway Administration 2006). The version of the FAF that we used (version 2.2) featured 114 U.S. domestic trade regions (including 63 major metropolitan areas in the conterminous U.S.), 17 additional U.S. ports of entry not specified as domestic regions, and seven international regions of origin (Fig. 1). Flows between FAF regions were reported, in both tonnage and monetary value, for 43 commodity categories (e.g., wood products, machinery) derived from the U.S.-Canadian Standard Classification of Transported Goods (SCTG).

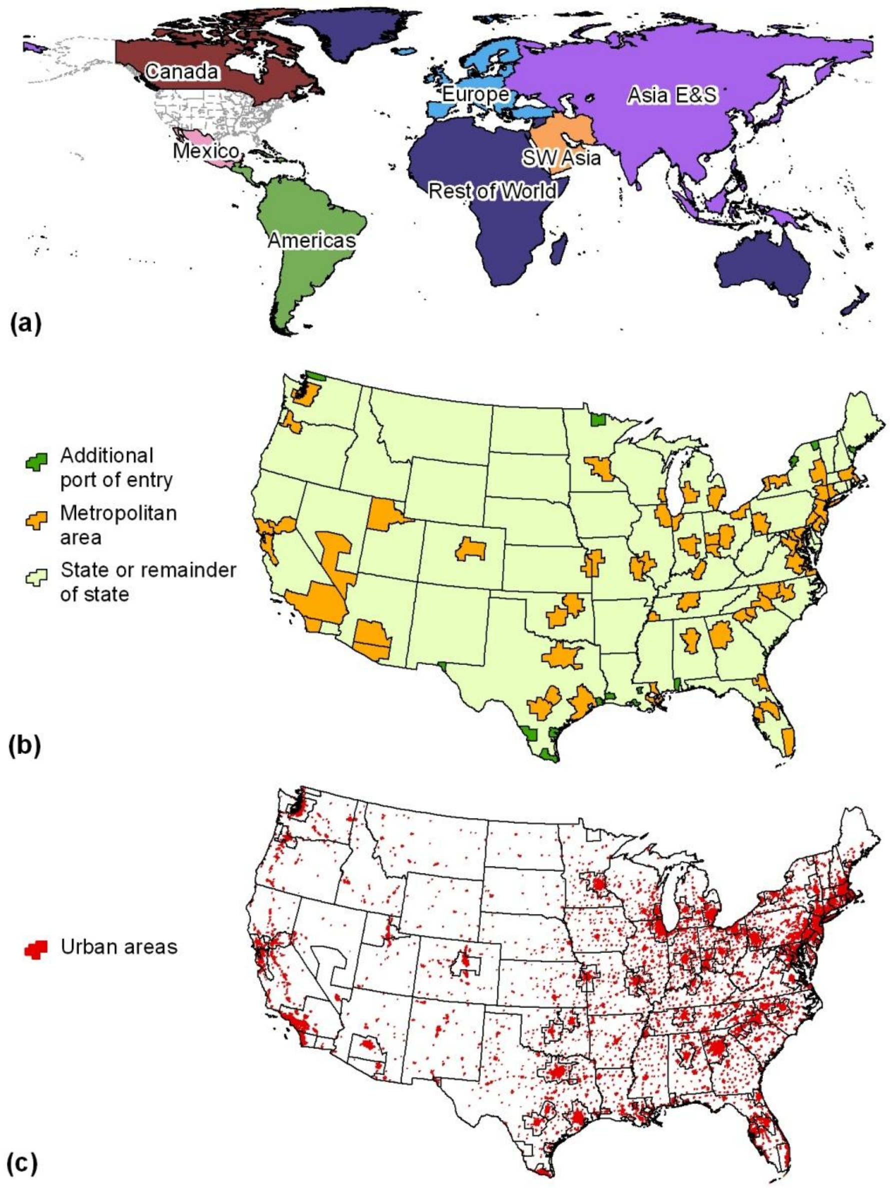

Figure 1. (a) World regions of origin in the international portion of the U.S. Freight Analysis Framework (FAF) database; (b) U.S. regions in the domestic portion of the FAF database; (c) urban areas defined by the U.S. Census Bureau.

Allocation protocols are described in detail in Koch et al. (2011). In essence, the process consisted of three analytical steps. In the first step, we used the “international” component of the FAF database to determine the tonnage of forest-insect-associated commodity imports arriving at each of the ports of entry from the world regions of origin (Fig. 1a). These import volumes were weighted in two ways: (1) by the proportional contribution of each origin region to the U.S. historical record of forest insect interceptions, determined through analysis of the PestID database; and (2) by the proportion of the imported tonnage of a given commodity that is composed of wood materials (estimated as 100% of the imported tonnage in the categories “logs and other wood in the rough” and “wood products”, and 10% of the imported tonnage in all other categories of interest).

In the second allocation step, we used the “domestic” component of the FAF database to determine the tonnage of forest-insect-associated commodities transported from the ports of entry to each of the 114 domestic trade regions (Fig. 1b). In the final step, we allocated the tonnages for the domestic trade regions to the individual urban areas within them (Fig. 1c). We did this based on the level of freight truck traffic associated with each urban area (determined with another component of the FAF database) as well as the human population level of the area. Finally, to estimate the annual alien forest insect species establishment rate for each urban area, we converted their tonnage values into proportions by dividing them by the total adjusted U.S. import tonnage from all origin regions, which we then multiplied by the nationwide forest insect establishment rate. We developed separate urban-area establishment rate estimates using FAF import projections for 2010 and 2020 (U.S. Federal Highway Administration 2006) as well as mean annual nationwide establishment rates for 2001-2010 and 2011-2020, respectively.

RESULTS AND DISCUSSION

Based on the re-parameterized log-linear model, we estimated the mean annual rate of alien forest insect species establishment for the U.S. to be 1.89 species per year for the period 2001-2010 and 1.7 species per year for 2011-2020. Thus, given current and projected U.S. import patterns, an average of ≈2 alien forest insect species are predicted to be established somewhere in the U.S. annually. Moreover, if we apply the "tens rule" of Williamson and Fitter (1996) to our estimates (i.e., 10% of newly established species will become an invasive pest that causes significant ecological and/or economic damages), this suggests that one new alien insect species will emerge as a noteworthy pest of U.S. forests every 5-6 years. Although these rates may not seem especially high, it is important to consider that a single established species could potentially have an economic impact on the order of tens of millions, or even billions, of dollars (e.g., Nowak et al. 2001).

The top two urban areas (out of 3,126) in terms of alien forest insect species establishment rate, for both 2010 (Fig. 2a) and 2020 (Fig. 2b), were Los Angeles–Long Beach–Santa Ana, CA and New York–Newark, NY-NJ-CT. The predicted rates for Los Angeles–Long Beach–Santa Ana, which were substantially higher than the rates for any other U.S. urban area (Table 1), mean that a new alien forest insect species would become established every 4-5 years in that area. By comparison, the estimated rates for New York–Newark project the establishment of a new forest insect species every 8-9 years. These are the two most populous U.S. 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 (U.S. Army Corps of Engineers Navigation Data Center 2007). Due to their population size and the corresponding demand for commodities, each of these two urban areas retains a large portion of its received imports, resulting in their relatively high predicted establishment rates. In fact, most urban areas in the top 25 (Table 1) 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 imports from Mexico, the other areas represent populous and/or highly connected nodes in the domestic commodity transportation network.

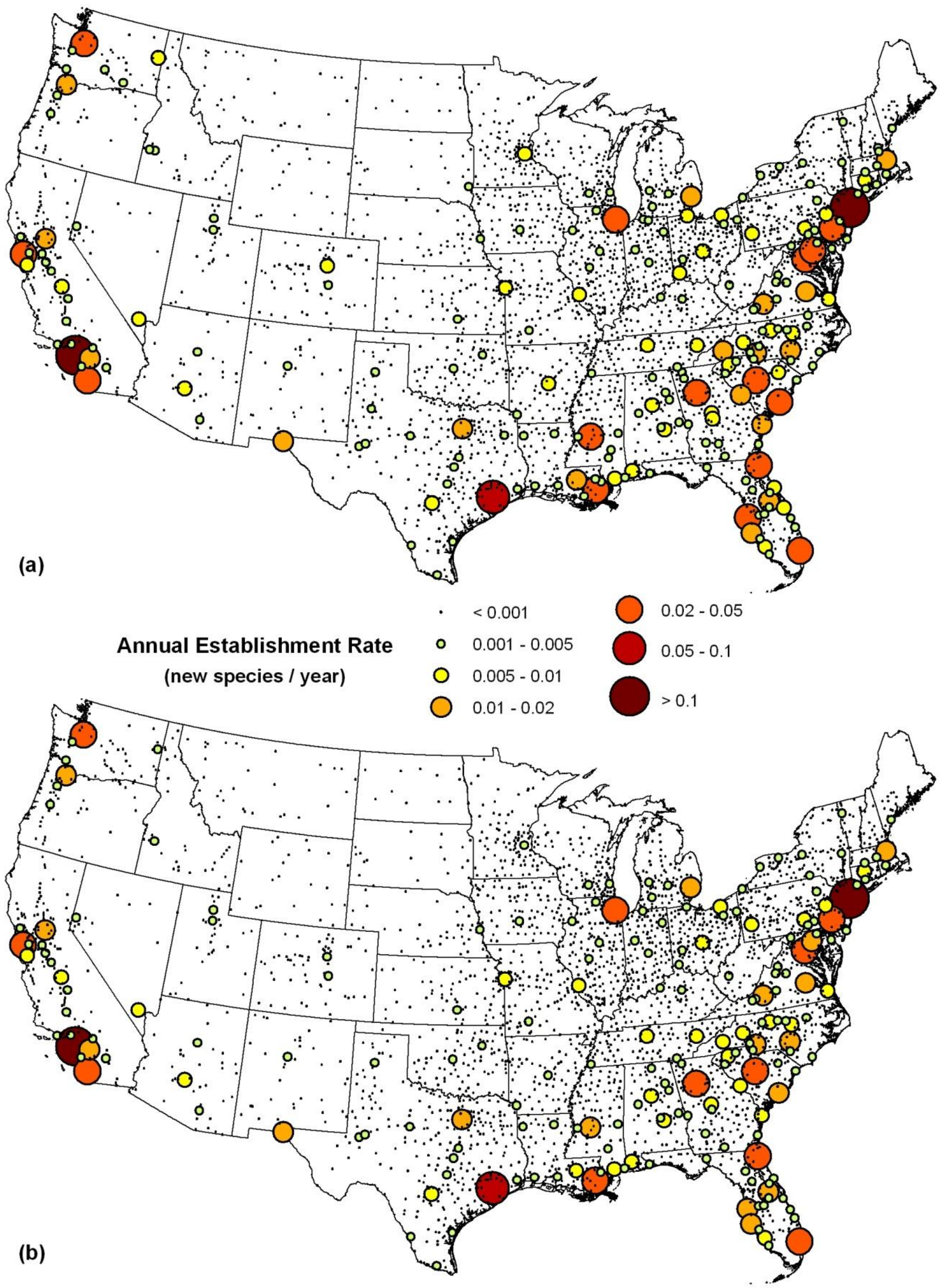

Figure 2. Annual alien forest insect species establishment rates in U.S. urban areas, based on relevant commodity imports from all world regions of origin: (a) rates estimated using 2010 FAF estimates and the 2001-2010 mean annual rate of alien forest insect establishment for the U.S. (1.89 species/year); (b) rates estimated using 2020 FAF projections and the 2011-2020 mean annual rate for the U.S. (1.7 species/year).

Table 1. Top 25 U.S. 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). Rates are based on FAF import projections for the years in question as well as species-accumulation estimates from a log-linear model.

	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)

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

Generally, the urban areas display minor changes in their predicted establishment rates from 2010 to 2020 (Table 1, Fig. 2). 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 small decreases in establishment rate between 2010 and 2020 (Table 1). Overall, our findings suggest that the next few decades could see a shift towards a greater proportion of forest invaders originating in Asia, especially given the current level of U.S. trade with China and other Asian countries (U.S. Department of Commerce 2010). This shift appears likely to be most relevant for California.

We think the analyses in this study have immediate relevance to decision makers responsible for implementing forest biosecurity strategies. Foremost, the establishment-rate geographic patterns captured here can serve as key input data for subsequent modeling of invasions of alien forest insect species. An important aspect of our 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 (i.e., number of new species per year) for our target group, alien forest insect species (Lockwood, Cassey, and Blackburn 2005). We also think the methodology can be readily adapted for other, non-forest sectors (e.g., agriculture and horticulture) or to analyze other dispersal pathways such as air passenger transport, which has been increasingly recognized for its role in the movement of invasive alien species (Hulme 2009; Liebhold et al. 2006; Tatem 2009).

STUDY II: DISPERSAL OF INVASIVE FOREST PESTS BY FIREWOOD MOVEMENT

In spatial models of invasions, dispersal processes are commonly modeled using dispersal kernels, which are probability density functions of the dispersal distances for an organism of interest. Long-distance dispersal processes, like the human-assisted transport of forest pests in firewood, typically require leptokurtic (or fat-tailed) probability density functions that are suited to representing the occurrence of rare events (Kot, Lewis, and van den Driessche 1996; Nathan et al. 2003). Because firewood is important as a potential long-distance vector, it would be useful if data were available as an empirical foundation for defining an appropriate distribution function to depict firewood dispersal potential. In this study, we had the opportunity to analyze a robust, multi-year data set about campground visitation patterns in the U.S. Our analysis had two objectives. First, we wanted to generally estimate the distance-dependent level of risk that a forest pest will be moved in firewood transported by campers for recreational use. Second, we wanted to explore similarities and differences between firewood-related dispersal functions derived for specific situations, such as for particular geographic regions or for certain types of origin or destination locations.

METHODS

Our principal data source for this study was the National Recreation Reservation Service (NRRS). The NRRS handles reservations for campgrounds and other recreational facilities that are operated by the U.S. Army Corps of Engineers, the Bureau of Land Management, the Bureau of Reclamation, the U.S. Forest Service, and the National Park Service. Members of the public (including individuals from outside the U.S.) can make reservations at these facilities through the NRRS online portal (http://www.recreation.gov), by telephone, or at specific field offices.

We acquired NRRS records spanning the time period from January 2004 to September 2009. Each NRRS record listed an origin location (i.e., visitor ZIP code) and a destination campground location, as well as the number of visitor reservations associated with that particular origin-destination combination. Prior to analysis, we deleted records associated with Alaska, Hawaii, Puerto Rico, and visitors from all foreign countries except Canada; in a study of firewood surrendered at Michigan's Mackinac Bridge, Haack, Petrice, and Wiedenhoeft (2010) noted firewood-carrying vehicles from three different Canadian provinces (Ontario, Alberta, and Newfoundland & Labrador). After this initial filtering, the data encompassed >7.2 million individual reservations made at 2,525 campgrounds and related recreational facilities.

For each record, we calculated the Euclidean distance between the visitor's origin ZIP code (i.e., the centroid of the ZIP code polygon) and the destination campground based on their geographic coordinates. We used kernel density estimation (Silverman 1986) to construct a basic empirical estimate of the probability density function of the visitor travel distances. We then fit the distance data with various theoretical distribution functions (e.g., lognormal, exponential, Cauchy) that have been previously applied to depict long-distance dispersal in spatial invasion models (Cannas, Marco, and Montemurro 2006; Carrasco et al. 2010; Pitt, Worner, and Suarez 2009). We fit these functions via maximum likelihood estimation, identifying the best-fitting function as the one with the lowest value of Akaike's information criterion (AIC).

We performed kernel density estimation and distribution-fitting for the entire data set, as well as for subsets of records associated with particular geographic regions (northeastern U.S., southeastern U.S., Midwestern U.S., and western U.S.). We similarly performed these procedures for two other subsets of the data: (1) records associated with campgrounds within 50 km of the 20 most visited U.S. national parks; and (2) records associated with visitors from the 20 most populous U.S. urban areas. For these latter two subsets, we also attempted to fit the data with mixture distribution functions (Higgins, Nathan, and Cain 2003; Nathan et al. 2003). In a spatial modeling context, a mixture distribution (or "mixed-kernel") approach assumes that a given distribution of dispersal distances may be better explained by a weighted combination of two or more theoretical distribution functions, each of which represents particular dispersal modes or categories (e.g., occasional overnight campers versus recreational vehicle users).

RESULTS AND DISCUSSION

Two major points emerged from our analysis of the NRRS data. First, the majority of campground visits involve short travel distances (Table 2), although it is not especially unusual for campers to travel a thousand kilometers or more to reach their destinations. In a map (Fig. 3) of the links between visitor origin ZIP codes and destination campgrounds, the highest-traffic links (i.e., the links with the highest numbers of reservations) are typically less than 250 km in length. Still, numerous instances of cross-country travel by campers are also evident.

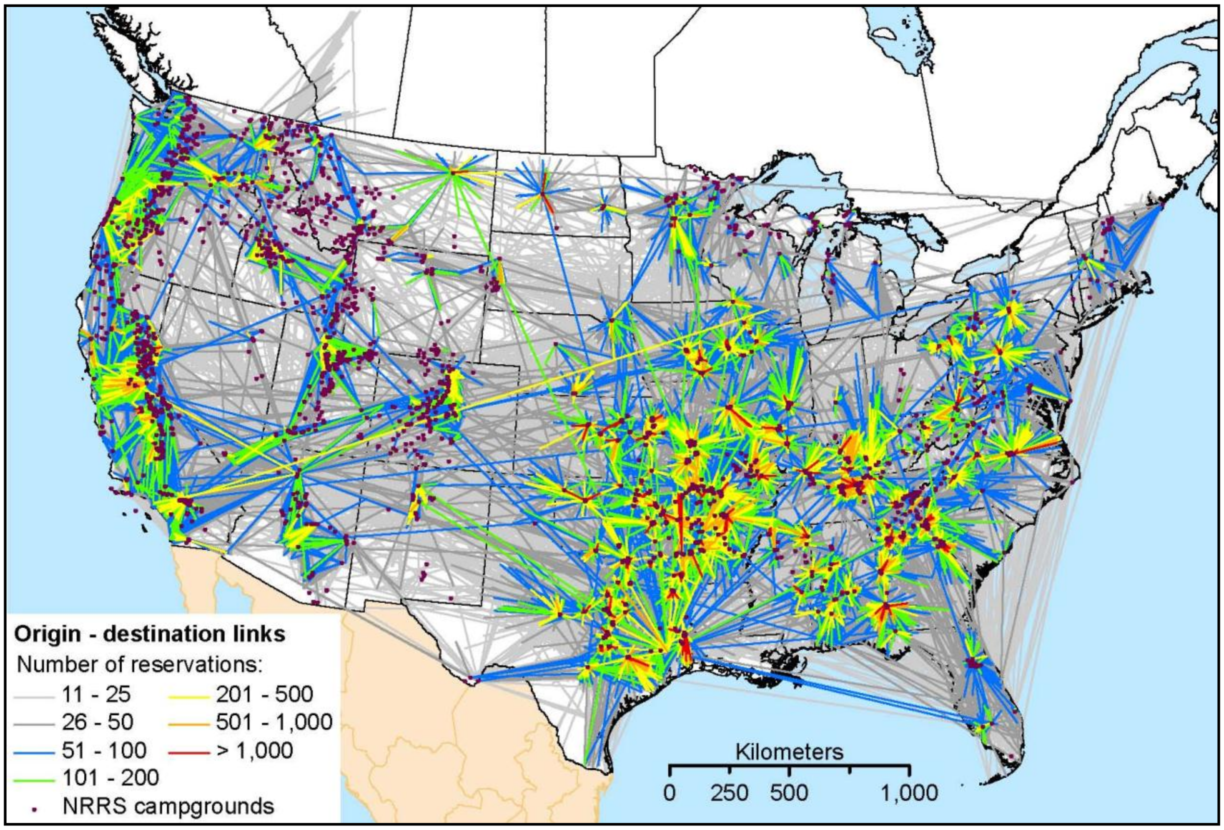

Figure 3. Map of the (straight-line) links between visitor origin ZIP codes and destination campgrounds for the full data set. The links have been classified according to their associated number of camper reservations. Links with fewer than ten reservations are not shown.

For the full data set as well as all of the geographic sub-regions except the western U.S., the median travel distance was less than 100 km. In contrast, the maximum travel distance in all sub-regions was greater than 3000 km, and for the full data set as well as the western and southeastern U.S., more than 5000 km. The mean travel distances in each region reflect some influence of longer-distance camper travel; for the full data set, ≈10% of visitors traveled more than 500 km or more, and ≈5% traveled more than 1000 km.

Table 2. Summary statistics about the distance distributions for the full data set and all tested subsets.

Region/category	Number of reservations	Median travel distance	Mean travel distance	Standard deviation	Maximum travel distance
Entire U.S.	7,220,563	92.6	235.8	463.2	5565.9
Southeastern U.S.	3,140,537	67.7	175.0	340.1	5565.9
Northeastern U.S.	358,584	85.3	180.4	364.4	4531.6
Midwestern U.S.	1,338,091	78.4	170.4	312.9	3279.5
Western U.S.	2,383,351	148.3	360.9	631.7	5435.9
20 most visited national parks	1,144,999	213.4	488.7	756.9	5435.9
20 most populous urban areas	1,117,898	171.6	370.7	605.5	4538.7

Second, we found that it was possible to achieve a good fit of the data using theoretical distribution functions. For the full data set and all of the subsets, the best-fitting theoretical distribution, based on minimum AIC, was the unbounded Johnson (or Johnson SU) distribution, followed closely by the lognormal distribution. For the full data set, a plot of density as estimated by the Johnson SU distribution versus the kernel density estimate suggests a very good fit across the entire range of travel distances (Fig. 4a). However, when the logarithm of density is plotted versus distance we observe slight over-prediction at distances between 500 km and 1000 km, and increasing under-prediction at distances greater than 1000 km (Fig. 4b). (Notice that the relative relationship between the Johnson SU and kernel density estimates is reversed on the logarithmic scale.) This pattern of under-prediction by the Johnson SU distribution at long travel distances generally holds true for each of the tested geographic sub-regions (Fig. 5), as well as for travel associated with the most visited national parks and most populous U.S. urban areas (not shown).

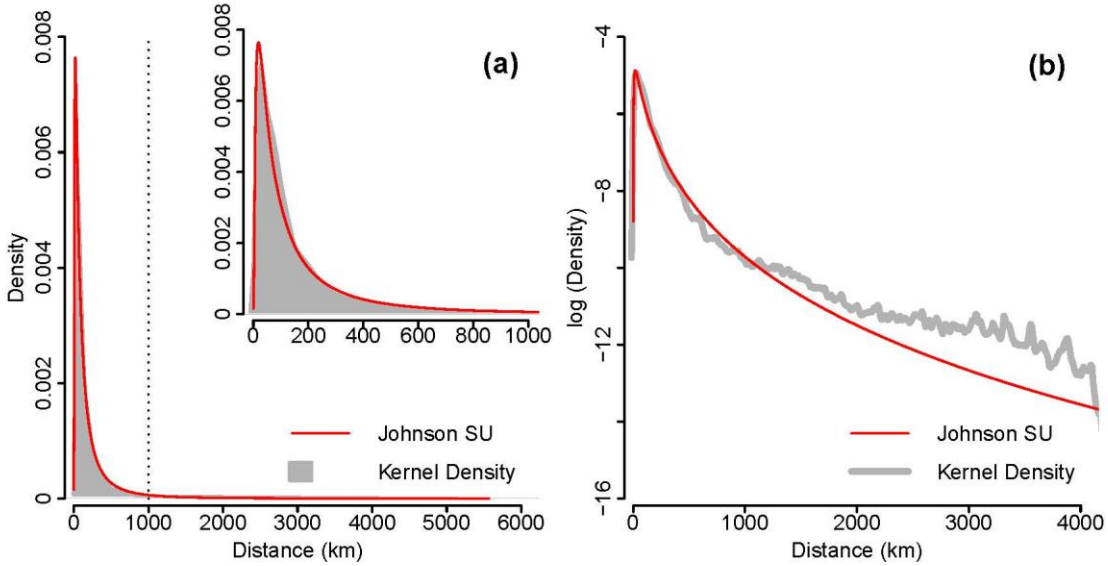

Figure 4. (a) Plot of density versus travel distance for the Johnson SU distribution and the kernel density estimate. Inset plot is a close-up showing distances < 1000 km; (b) plot of log(density) versus travel distance for the Johnson SU distribution and the kernel density estimate. Curves are based on the full data set.

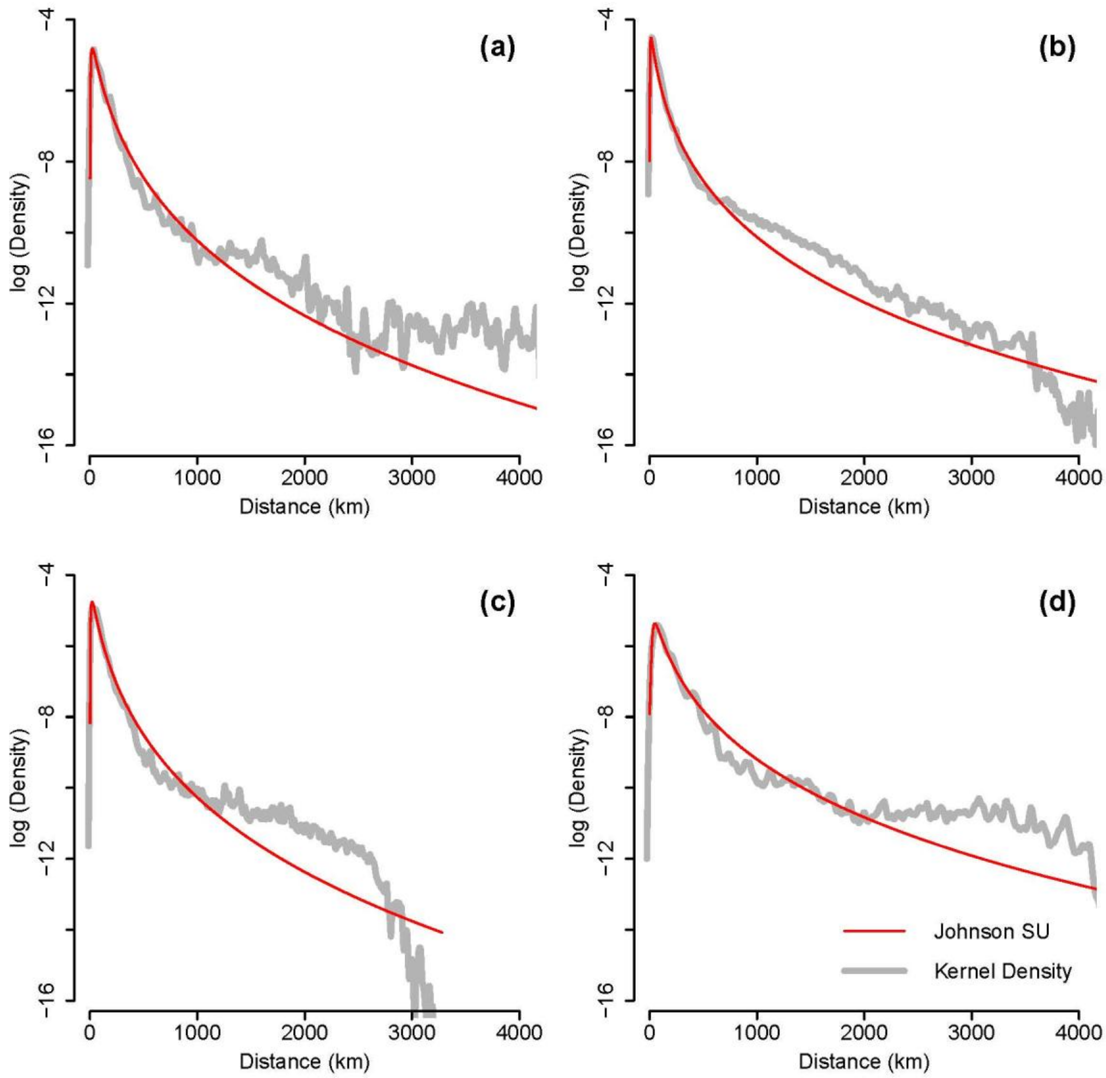

Figure 5. Plots of log(density) versus travel distance for the Johnson SU distribution and the kernel density estimate, based on data for four geographic sub-regions: (a) Northeastern U.S.; (b) Southeastern U.S.; (c) Midwestern U.S.; (d) Western U.S.

Arguably, campers who travel long distances are unlikely to carry firewood, so under-prediction by the Johnson SU or any other theoretical distribution at these long distances may not be of concern. Nevertheless, mixture distributions may present a better alternative fitting approach. As an illustration, Figure 6 shows a three-component lognormal mixture distribution applied to the data subset associated with the 20 most visited U.S. national parks. In addition to providing better fit, this type of mixture distribution may also better represent differences between certain categories of dispersal. For example, the individual component distributions comprising the mixture in Figure 6 may be interpreted as corresponding to three types of campground visitors: the large majority of overnight campers, whose travel times are typically less than a couple of hours (component 1); campers visiting specific destination campgrounds (i.e., specific national parks) who are thus willing to travel farther (component 2); and campers with longer-term itineraries, perhaps involving the use of recreational vehicles and visits of multiple locations (component 3). Campers in each of these categories probably have different likelihoods of transporting firewood with them.

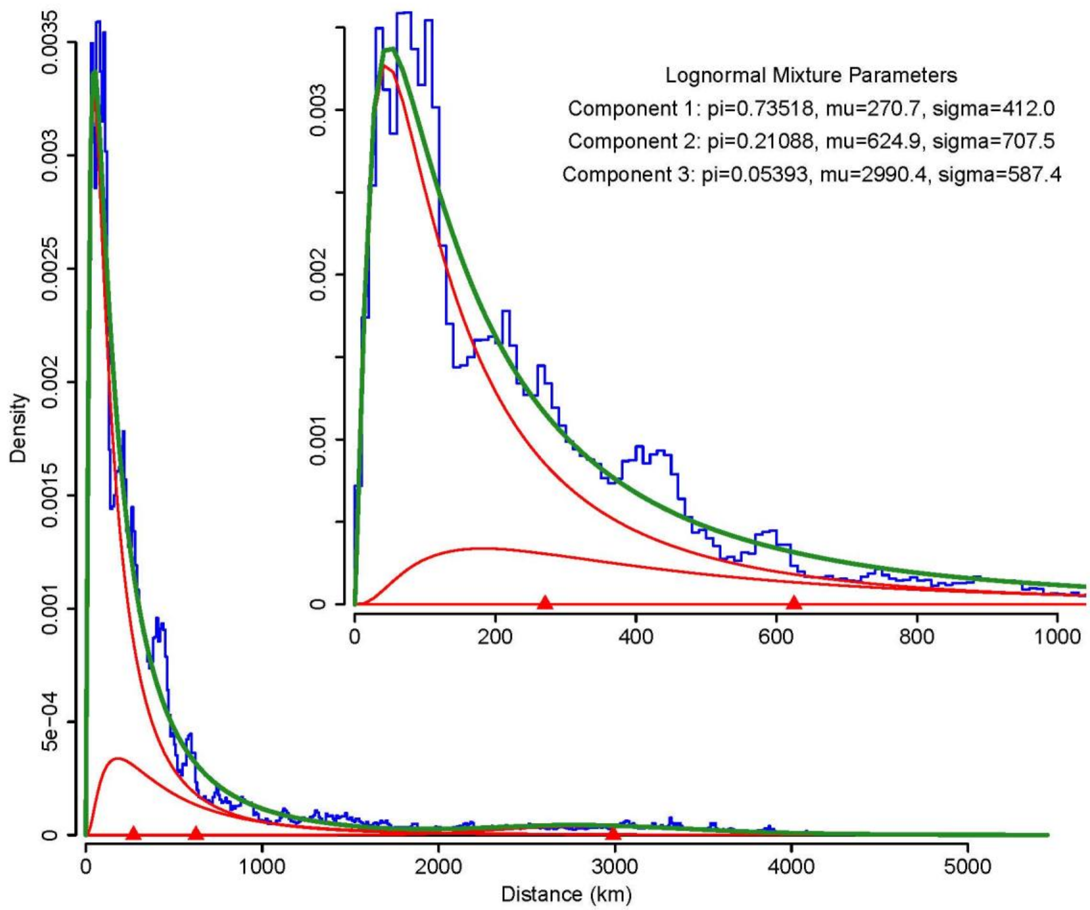

Figure 6. Plot of a three-component lognormal mixture distribution for the data subset associated with the 20 most visited U.S. national parks. Inset is a close-up of distances < 1000 km. For each component distribution, the parameter pi represents the component's proportional contribution to the entire mixture, mu is the mean of the component distribution, and sigma is its standard deviation.

With respect to the second point, and regardless of the chosen distribution function, creating a realistic dispersal kernel from the NRRS data requires an estimate of the likelihood that a given camper is carrying pest-infested firewood. Unfortunately, there have been few firewood usage surveys, and those that have been done have been limited in sample size and geographic scope (Haack, Petrice, and Wiedenhoeft 2010; U.S. Department of Agriculture-Animal and Plant Health Inspection Service 2010). We conducted a preliminary estimation of available data indicating that 6-10% of campground visitors transport firewood infested with viable forest pests (assuming a low likelihood of firewood transport at longer travel distances). If we account for other factors such as the burning of firewood before pests can escape, then 3-5% of campground visits potentially pose a high risk of firewood-mediated dispersal of forest pests. If we applied this relatively small risk factor as a modifier to any dispersal kernel derived from the NRRS data, it would considerably increase the long-distance dispersal potential of any forest pest of interest beyond its natural spread capabilities. Hence, current concerns about the risk of forest pest spread in camper-transported firewood appear to be justified. Further work is underway to elucidate whether these findings can be translated to represent other modes of accidental, human-mediated dispersal of invasive species (e.g., the movement of potentially infested nursery stock for landscaping purposes, or the movement of firewood for home heating).

IMPLICATIONS AND FUTURE DIRECTIONS

Predicting which species are likely to become major pests is a common starting point when developing an invasive species management strategy (Kolar and Lodge 2001; Reichard and Hamilton 1997). Yet, many species are not immediately identifiable as threats to the places they invade (Crooks 2005; Williamson and Fitter 1996). Therefore, an effective predictive system must also anticipate where, and at what rate, invaders are most likely to become established as pests, thus offering a way to prioritize surveillance efforts and response measures (Magarey, Colunga-Garcia, and Fieselmann 2009; Meyerson and Reaser 2002).

The two studies described in this paper represent our first attempts to develop predictive systems that properly account for the disproportionate role of human-mediated dispersal pathways in facilitating biological invasions. The results of each study, however, provide only partial answers. Further work is necessary to apply our findings effectively. For instance, our two studies only deal with specific human-mediated dispersal processes. If a spatial model is to provide realistic predictions regarding an invasive pest of interest, these dispersal processes would have to be integrated with other dispersal processes (e.g., "natural" dispersal) that also determine how the pest is likely to expand its range.

Furthermore, a number of steps may be taken to directly improve the applicability of our findings. For example, with respect to the first study, the abundance and connectivity of host tree stands within an urban area 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, Haack, et al. 2010). 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.

In the second highlighted study, we showed that the distributions of camper travel distances from the NRRS data varied according to particular regional or category-specific (e.g., associated with the most visited national parks) travel patterns. Perhaps more importantly, any dispersal function that might be developed from these distributions can only be reasonably applied in a targeted fashion; essentially, the dispersal of invasive species in transported firewood will only occur at specific locations connected by the system of camper travel routes. Given these conditions, it seems most appropriate to analyze the data, and generate outputs, in a networked setting. For a recently initiated study, we have represented visitor home and campground locations as two sets of linked nodes, with the strength of each link defined by the number of campers traveling along it. We can then apply a probabilistic pathway model to the network to identify major vectors of forest insect spread via recreational firewood movement. Repeated model simulations will yield probabilistic estimates of the most likely pathways and destinations for a forest insect introduced at any origin node. Furthermore, the results will provide probabilistic estimates of the most likely origins for any destination node found to be invaded, which could substantially improve early detection efforts. We also think this networked approach can be applied to trade pathways, although such an analysis is likely to be much more computationally intensive, especially if it involves international commodity transportation networks.

In summary, adding a realistic human-mediated dispersal component will improve the predictive capabilities of any spatial model for an invasive species, not least by serving to close some important information gaps regarding the invader. While not necessarily targeted at invasive species, data sets that describe pathways of trade and transportation may be creatively adapted to address those information gaps. We think this is a potentially fruitful area of research, and so we are greatly interested in collaborating with other scientists who perceive further potential applications of trade and transportation data to invasive species problems.

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BIOGRAPHICAL SKETCH

Frank Koch is currently a Research Ecologist with the USDA Forest Service – Eastern Forest Environmental Threat Assessment Center (Research Triangle Park, NC). Previously, he was a Research Assistant Professor with the NC State University Department of Forestry and Environmental Resources. Dr. Koch's primary area of research is alien forest pest invasions. Specifically, he is interested in methods to translate species' biology and behavior into spatially explicit characterizations of invasion risk pattern (i.e., pest risk maps). Dr. Koch has contributed to the development of national-scale risk maps for insects such as the sirex woodwasp (*Sirex noctilio*) and redbay ambrosia beetle (*Xyleborus glabratus*) and pathogens such as *Phytophthora ramorum* and *P. alni*. He has also completed research on ways to quantify and represent the effects of uncertainty in invasion risk maps and their underlying models. As described in this paper, Dr. Koch has most recently been collaborating with other scientists on the use of trade and transportation networks to estimate invasion likelihoods for specific locations of interest. He has a BA (Art Design / Philosophy) from Duke University as well as an MS (Natural Resources) and PhD (Forestry) from NC State University.

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