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Anthropogenic drivers of gypsy moth spread

Kevin M. Bigsby · Patrick C. Tobin · Erin O. Sills

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Abstract The gypsy moth, *Lymantria dispar* (L.), is a polyphagous defoliator introduced to Medford, Massachusetts in 1869. It has spread to over 860,000 km^2 in North America, but this still only represents ¼ of its susceptible host range in the United States. To delay defoliation in the remaining susceptible host range, the government maintains a barrier zone and a quarantine, reflecting a presumption that anthropogenic factors are important in the spread of gypsy moth. We develop a model framework that relates these factors along with biophysical characteristics to a county's susceptibility to gypsy moth invasion. We then compile a dataset for counties within 200 km of the infested area and use trap catch data from 1999 to 2007 to estimate the probability of gypsy moth presence. As expected, gypsy moth is more likely to be found close to the population front and to traps that recorded moths in the previous year. However, when controlling for these factors, our most robust finding is that the use of wood for home heating and energy is consistently positively correlated with the presence of gypsy moth. In contrast, the movement of wood products by industry, which is actively regulated by state and federal governments, is rarely correlated with the presence of gypsy moth. This is consistent with effective regulation of the movement of goods by industry, but not by the public. Our findings provide empirical support for the importance and challenge of firewood as a vector for non-native forest insects.

Keywords Anthropogenic dispersal · *Lymantria dispar* · Firewood · Non-native species · Spread

K. M. Bigsby (✉) · E. O. Sills
Department of Forestry and Natural Resources, North Carolina State University, 3120 Jordan Hall, Raleigh, NC 27695, USA
e-mail: kmbigsby@ncsu.edu

P. C. Tobin
United States Department of Agriculture, Forest Service, Northern Research Station, 180 Canfield Street, Morgantown, WV 26505, USA

Introduction

Biological invaders are significant threats to the function and composition of forests, resulting in considerable economic and ecological costs (Mooney and Cleland 2001; Pimentel et al. 2005). The introduction of non-native species into novel environments has increased dramatically with increases in global trade and travel (di Castri 1989; National Research Council 2002; Work et al. 2005; Brockerhoff et al. 2006). Once introduced, non-native species often spread through stratified dispersal in which local population growth and diffusive spread is coupled with long-range dispersal (Hengeveld 1989;

Shigesada et al. 1995). Stratified dispersal has been observed and quantified in many invasive species (e.g., Mack 1985; Okubo et al. 1989; Andow et al. 1990; Sharov and Liebhold 1998). Humans tend to play an important role in the long-range dispersal of biota (Ruiz et al. 2000; Gilbert et al. 2004; Muirhead et al. 2006). This has motivated efforts to model those anthropogenic factors, such as through gravity models (Bossenbroek et al. 2001; Drake and Lodge 2004; Leung et al. 2006). In this paper, we examine the role of anthropogenic factors in the spread of the gypsy moth, *Lymantria dispar* (L.), in a transition zone extending from the gypsy moth's established range up to 200 km away, where both diffusive spread and long-range dispersal are at play. In this zone, we find a positive association between household use of wood for heating and energy and the probability of invasion by the gypsy moth.

The gypsy moth was first introduced to North America in Medford, Massachusetts, US in 1869 (Liebhold et al. 1989) and is now established in parts of 19 US states and five Canadian provinces (Fig. 1a; Tobin et al. 2009). Federal and state governments in the US invest considerable resources in the management of gypsy moth due to the significant negative impacts of outbreaks (e.g., Campbell and Sloan 1977; Tuthill et al. 1984; Jakus 1994; Thurber et al. 1994; Leuschner et al. 1996; Davidson et al. 1999; Redman and Scriber 2000; Mayo et al. 2003). Management efforts include both eradicating populations that arise far outside of the infested area and suppressing outbreaking populations in the infested area. In a transition zone between these two areas, management focuses on reducing rate of spread (Tobin and Blackburn 2007), effectively delaying the costs associated with gypsy moth outside the infested area (Leuschner et al. 1996). Within this transition zone, new gypsy moth infestations occur along the leading edge of the population front but also up to 200 km away from the leading edge (Sharov and Liebhold 1998; Tobin and Blackburn 2008).

The movement of any biological invader, including the gypsy moth, occurs through invasion pathways, which are routes through which an invasive

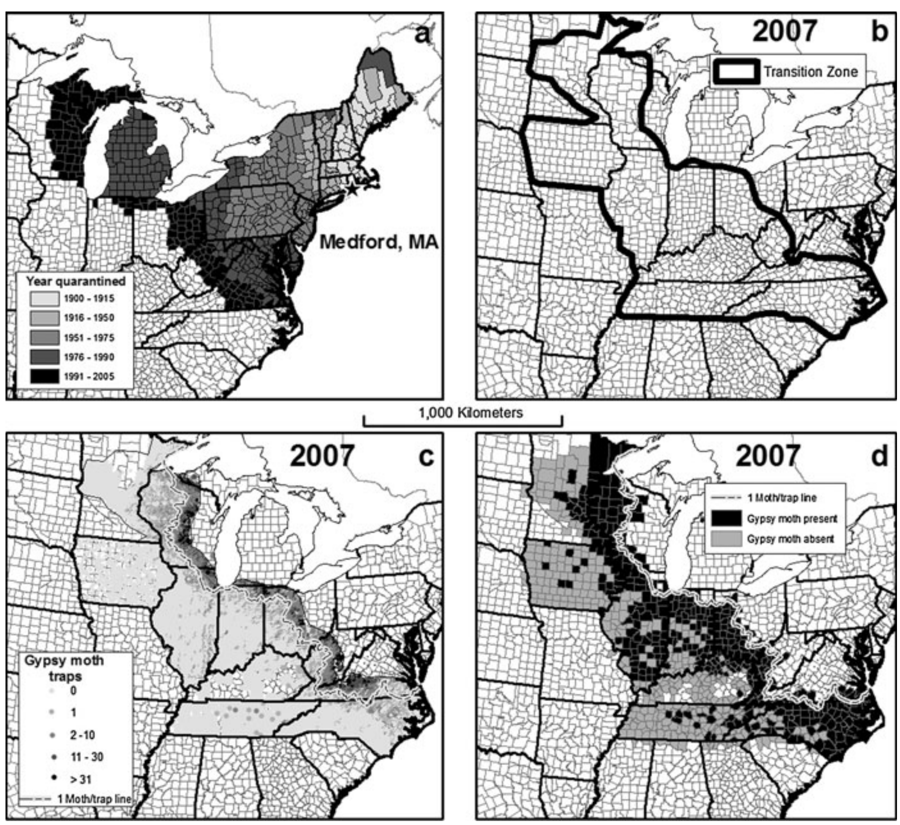

Fig. 1 **a** Spatial time series of the gypsy moth invasion in the United States, 1900–2005. **b** Within a transition zone between established and unestablished areas, approximately 100,000 pheromone-baited traps are deployed annually under the Slow-the-Spread program to detect new gypsy moth populations that arise within this zone. **c** Counts of gypsy moth males recorded from traps in 2007. Counts are used to derive the one moth per trap population boundary. **d** For counties inside the transition zone and ahead of or intersecting the one moth per trap boundary, we generated a binary dependent variable indicating presence or absence of gypsy moth based on the annual trap catch data in each county (2007 data shown as an example)

species is transported from a source population to a recipient location on a transport vector (e.g., firewood, nursery stock, or industrial wood products) (Lockwood et al. 2007). Invasion pathways can be characterized as either anthropogenic, such as shipping routes, or natural, such as atmospheric transport mechanisms (Kiritani and Yamamura 2003; Hulme et al. 2008). The natural invasion pathway for gypsy moth is through early instar ballooning and adult male flight (i.e., diffusive spread). Liebhold et al. (1992) used demographic data to parameterize a Skellam model (Skellam 1951) and estimated gypsy moth diffusive spread to be 2.5 km per year; however, empirical distributional data suggested spread rates >20 km per year. This points to the importance of anthropogenic invasion pathways, or the unintentional movement of life stages by humans (Mason and McManus 1981; Elkinton and Liebhold 1990; Liebhold and Tobin 2006).

Anthropogenic movement of gypsy moth life stages is believed to play an important role in long-distance dispersal of gypsy moth (Mason and McManus 1981; Sharov et al. 1997; Liebhold and Tobin 2006). The egg mass is the life stage most likely to be moved by humans because it is present for approximately 8 months, is sessile, and as the dispausing stage it is preconditioned to survive long treks. Thus, human transport of goods on which egg masses have been oviposited is an important invasion pathway (Hajek and Tobin 2009). However, attempts to precisely quantify the importance of various routes and vectors, and the underlying anthropogenic factors, are surprisingly limited. Lippitt et al. (2008) is one of the few previous studies that modeled the influence of anthropogenic factors on the probability of gypsy moth being introduced outside of its established range. They focused on introduction of the gypsy moth far from its established range, where diffusive spread is unlikely to play a role. In contrast, we specify and estimate a model of the probability of gypsy moth being introduced within a transition zone where spread through both diffusive and anthropogenic invasion pathways is likely.

Materials and methods

Study area

The Slow-the-Spread program monitors gypsy moth populations along the leading edge of the population front using ≈100,000 pheromone-baited traps spaced between 2 and 8 km and deployed during the period of male moth flight. Trap records are used to delineate various population boundaries and to define the boundaries of the Slow-the-Spread program in subsequent years (Tobin and Blackburn 2007). In general, traps are placed in an ≈170 km wide band, where ≈¼ of all traps are behind the population boundary at which one male moth is recorded per trap (the "one moth per trap line," i.e., in the infested area) and ≈¾ of all traps are in front of the one moth per trap line (i.e., in the uninfested area). Additional traps are also placed in areas outside of the Slow-the-Spread trapping area. The number of these additional traps, however, varies from year to year depending on the level of funding available. We used trap catch data from both the Slow-the-Spread trapping area and these outside areas to define the boundaries of our study area (Fig. 1b). Thus, the spatial extent of our study area changed from year to year, from 432 to 790 counties or 650,000–1,100,000 km^2 over the time period considered, 1999 through 2007 (Table 1). The entire study area was within the suitable climate zone for gypsy moth (Grey et al. 2007). Trap catch data (Fig. 1c) were aggregated to presence or absence (Fig. 1d) at the county level, primarily for

Table 1 The number of counties monitored through the Slow-the-Spread program and used in our analyses

Year	1999	2000	2001	2002	2003	2004	2005	2006	2007
Number of counties included in analysis	499	534	465	472	528	559	432	769	790
Number of counties with gypsy moth present	297	302	261	244	221	290	164	441	371
Percent of counties with gypsy moth present	59.5	56.6	56.1	51.7	41.9	51.9	38.0	57.3	47.0

compatibility with county-level data on anthropogenic variables available through the U.S. Census.

Model framework

We consider both natural diffusion (e.g., larval ballooning and adult male moth flight) and human-assisted movement as pathways of gypsy moth spread in the transition zone. The probability of formation of new colonies through diffusive spread is likely to be most strongly influenced by proximity and size of source populations. Anthropogenic movement involves more steps, beginning when gypsy moth females, which do not fly, oviposit on objects that people then transport from the infested area into the transition zone, either as personal goods carried by households or commercial goods that are shipped into or transshipped through the transition zone. For example, these objects could include recreational equipment, vehicles, or wood.

Because we do not have data on the number of people or volume of shipments that travel from the infested area to counties in the transition zone, we instead focus on the characteristics of counties in the transition zone that are likely to influence these movements. We group these into three broad anthropogenic categories: (1) the amenities that attract visitors to the county, (2) the transportation network, which affects the movement of people and goods into and through a county, and (3) the demand for goods in a county. Within these categories, we specifically sought to include variables likely to proxy for or influence the movement of objects subject to the quarantine (USDA APHIS 2006). In addition to the anthropogenic factors we also consider three broad biophysical categories that potentially influence both diffusive spread and long-distance spread, through interactions with anthropogenic factors: (1) proximity to outbreak areas, (2) population distribution, and (3) ecophysical characteristics. For each category, we compiled data on the variables listed in Table 2 for each county in the transition zone.

Human population both in and near a given county is important for anthropogenic spread. We constructed a gravity variable for each year that captures the connectivity between county pairs based on population density and distance. This required first constructing a matrix of connectivity between all uninfested counties j in the transition zone and all infested counties i under quarantine, denoted as C_{ij}, according to:

$$C_{ij} = \frac{\ln(\text{pden}_i)(\text{pden}_j)}{\ln(D_{ij})}, \quad (1)$$

where pden are the population densities of counties i and j, and D_{ij} is the Euclidean distance between county i and j. We then multiply the resulting pairwise matrix of values for C_{ij} by a vector indicating presence or absence of gypsy moth in counties in the previous year, P_{t-1}, to estimate the gravity variable in year t, G, according to:

$$[G_t] = [P_{t-1}] * [C_{ij}]. \quad (2)$$

We initially considered two approaches to represent the density and distribution of human population. One was to use a series of demographic characteristics including population density and the distribution of the population between rural and urban areas. However, preliminary models suggested that the gravity variable described in Eqs. 1, 2 had more explanatory power and suffered less from multicollinearity with other variables in the model. The gravity variable is constructed using Euclidean distances, which are considered to be reasonable at a large spatial scale (Drake and Mandrak 2010). Therefore, this variable may capture natural dispersion of the gypsy moth, such as through larval ballooning and adult male flight, as well as transport by people along road networks.

Data analyses

Our model framework suggests that the probability of observing gypsy moth in a given county in the transition zone in a given year depends on six different categories of anthropogenic and biophysical factors. Because we have multiple candidate variables in each category with some redundancy and collinearity among them, we first employed stepwise logistic regression within each category in each year to empirically select variables for the final models. Variables that were significant ($P < 0.05$) in more than 1 year were selected for the full model. To assess the robustness of this model, we also specified a reduced model that included the two variables from each anthropogenic and biophysical category that were significant in the most number of years.

Table 2 Summary of the anthropogenic and biophysical variables, grouped into three broad anthropogenic (A) and three broad biophysical (B) categories, used in our analyses

Variable	Definition; source; year	Unit	Mean	SD
Supply of amenities (*A*)				
Recreational counties	Binary indicator of a county's status as recreation dependent based on economic criteria; USDA Economic Research Service; 2004	Binary	NA	NA
Park area	Total area of all state and national parks; Tele Atlas North America; 2006	km^2	16.57	66.55
Campgrounds	Number of individual camp sites from Forest Service, US Army Corp of Engineers, Bureau of Land Management, and Tennessee Valley Authority; National Outdoor Recreation Supply Information System; 1997	Count	0.01	0.07
Picnic areas	Number of individual picnic sites from Forest Service, US Army Corp of Engineers, Bureau of Land Management, and Tennessee Valley Authority; National Outdoor Recreation Supply Information System; 1997	Count	6.94	29.61
Seasonal homes	Housing units intended for occupancy only during certain seasons of the year and found primarily in resort areas. This also includes housing units used for migratory labor employed during a crop season and seasonal mobile homes; US Census Bureau; Decennial Census; 2000	1,000 of homes	0.75	1.74
Retirement counties	Binary indicator of a county's status as retirement dependent based on economic and demographic criteria; USDA Economic Research Service; 2004	Binary	NA	NA
Migration[a]	Number of people immigrating to emigrating from a county including births and deaths; US Census Bureau, Population Division; 1999–2007	Count	0.02	0.28
Mean distance to nearest road	Mean distance of all locations in a county to the nearest road; USGS (Watts et al. 2007); 2007	km	0.31	0.47
Transportation (*A*)				
Rest areas	Number of rest areas, visitor welcome centers, or scenic vistas; POI Factory; 2007	Count	0.46	0.90
Railroad distance	Length of railroads; Federal Railroad Administration; 2006	km	0.07	0.07
Airports	Number of airports; Federal Aviation Administration; 2004	Count	4.86	5.06
Highway distance	Length of major and minor US highways and roads; US Department of Commerce; 1998	km	223.60	115.92
Demand for goods[b] (*A*)				
Gravity	A metric that represents the population density and proximity of county pairs to the location of counties in quarantine for gypsy moth; derived by researchers; 1999–2007	Metric	4.00	6.29
Income	Median household income; US Census Bureau, Population Division; 2000	1,000 USD	35.94	7.91
Nurseries	Area of nurseries, greenhouse, etc. under glass or other protection; USDA National Agriculture Statistical Service; 2002	km^2	14.65	23.58
Open nurseries	Total area of nurseries, greenhouse, etc.; USDA National Agriculture Statistical Service; 2002	km^2	0.88	3.61
Sawmills	Number of composite, plyven, postpole, pulpmill, and other sawmills (firewood, bark products, charcoal); USDA Forest Service; 2004	Count	2.57	3.17
Household wood	The number of households that use wood or wood charcoal as a primary heating fuel; US Census, American Housing Survey; 2005	1,000 households	0.45	0.40

Table 2 continued

Variable	Definition; source; year	Unit	Mean	SD
Household wood/population	Ratio of household wood to population; US Census, American Housing Survey; 2005	Wood/population	0.16	0.17
Household wood/area	Ratio of household wood to area; US Census, American Housing Survey; 2005	Wood/km^2	16.30	26.42
Big box retailers	Number of Wal-mart and Sams clubs; POI Factory; 2007	Count	1.17	2.00
Christmas tree farms	Total area of Christmas tree farms; USDA National Agriculture Statistical Service; 2002	km^2	0.03	0.07
Source infestation (*B*)				
Size of outbreak within 100 km (1 year lag)[a]	Total area of defoliation within 100 km of county centroids. Data was lagged 1 year, e.g., defoliation in 1998 corresponds to gypsy moth trap results in 1999; Slow-the-Spread; 1998–2006	km^2	0.61	3.62
Size of outbreak within 100 km (4 year lag)[a]	Total area of defoliation within 100 km of county centroids. Data was lagged 4 years, e.g., defoliation in 1995 corresponds to gypsy moth trap results in 1999; Slow-the-Spread; 1995–2004	km^2	0.61	3.62
Lagged distance to outbreak (1 year)[a]	Distance from nearest defoliation to county centroids. Data was lagged 1 year; Slow-the-Spread; 1998–2006	km	665.33	415.89
Lagged distance to outbreak (4 year)[a]	Distance from nearest defoliation to county centroids. Data was lagged 4 years; Slow-the-Spread; 1995–2004	km	665.33	415.89
Population distribution (*B*)				
Distance to 1 moth per trap line[a]	Distance from each county's centroid to the 1 moth/trap line; Slow-the-Spread; 1999–2007	km	207.12	158.56
Treatment	Size of aerial and other treatments to eradicate gypsy moth populations; Slow-the-Spread; 1999–2007	km^2	1.91	15.13
Lagged positive trap	Binary indicator of gypsy moth presence in a previous year based on proximity to gypsy moth positive traps. Any county within 2.5 km of a gypsy moth present trap is positive; Slow-the-Spread; 1998–2006	Binary	NA	NA
Ecophysical (*B*)				
Susceptible basal area	Proportion of land area covered by tree species susceptible to gypsy moth (>20% basal area in preferred species); USDA Forest Service; 1995	Percent	0.19	0.18
County latitude	The latitude of a county's centroid	NA	NA	NA
County longitude	The longitude of a county's centroid	NA	NA	NA
County area	Total area of a county; US Census TIGER file; 2007	km^2	1,404.55	979.95
Dependent variable				
Presence/absence	Presence or absence of gypsy moth; Slow-the-Spread; 1999–2007	Binary	NA	NA

[a] Indicates variables are year dependent and values are presented for 2007 as a reference

[b] Because the gravity variable is used in all models the population variables (urban and rural population, population density, urban population inside urban areas and clusters of urban population) are not displayed

Spatial autocorrelation was another potential concern with the estimation, because the trap catch data are known to be spatially correlated (Sharov et al. 1996). Spatially autocorrelated data can complicate tests of significance due to the violation of the assumption of independence (Clifford et al. 1989). A semivariogram of the Pearson χ^2 residuals from a model with only variables from the anthropogenic categories, clearly showing that values that are closer together are more similar than those that are further apart and that there is a distinct sill or threshold at which spatial dependence is no longer observed, is illustrated in Fig. 2a. The addition of biophysical variables, such as distance to an estimated population boundary, the one moth per trap line, partly addresses this issue. We also added latitude and longitude of

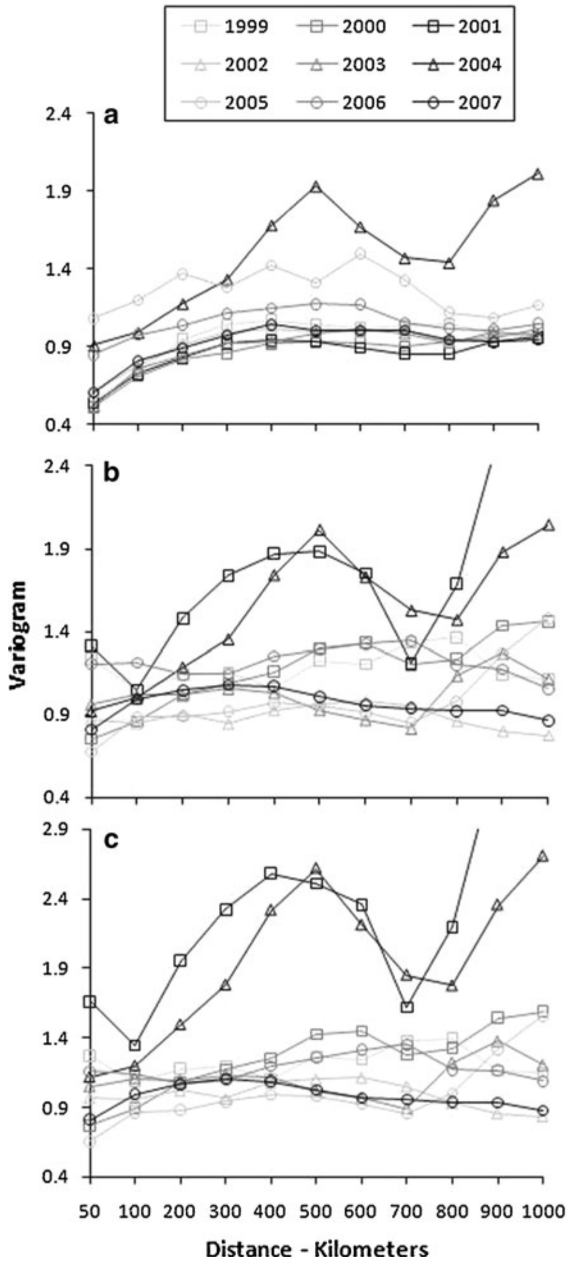

Fig. 2 **a** The semivariance of Pearson χ^2 residuals for logistic regression models with variables from the anthropogenic categories when excluding variables accounting for the spatial dependence of gypsy moth populations. **b** The semivariance of Pearson χ^2 residuals for the full model of gypsy moth spread. Note how spatial autocorrelation is reduced by adding covariates of spatial depency including county latitude and longitude. Pearson correlation coefficients of model residuals and distance to the one moth per trap boundary are significant for all years ($P < 0.05$) in the models without spatial variables, while they are significant only 2 year in the full model and 3 years in the reduced model. **c** The semivariance of Pearson χ^2 residuals for the reduced model of gypsy moth spread. Model residuals are similar to the full model **b**, indicating we have selected a robust model

county centroids to both the full and reduced model specification. We confirmed that this relatively simple fix addressed the concerns of spatial autocorrelation by checking semivariograms of the full and reduced model Pearson χ^2 residuals (Fig. 2b, c).

To interpret the logistic estimation results in the final models, we considered the number of years each variable was significant ($P < 0.05$) or nearly significant ($P < 0.10$), the sizes of the coefficients, and odds ratios estimates. All data analyses were conducted in SAS 9.1 (SAS Institute 2010).

Results

Model selection

The results of the step-wise logistic regressions used to develop the final empirical specifications are summarized in Table 3. For each biophysical and anthropogenic category, the table indicates the number of years that each component variable was significant and the range of pseudo R^2 values, which we interpret as a coarse summary statistic describing the overall significance of each category. Several variables were significant in 8 or 9 years, including the number of airports in the county, use of wood as a household energy source, and distance to a gypsy moth outbreak in the prior year. The population distribution category was overall the strongest predictor of gypsy moth presence (pseudo R^2 range of 0.43–0.64). In this category, two variables were significant in every year: (1) distance to the one moth per trap line, and (2) whether or not a county was within 2.5 km of a trap recording at least one male moth last year. Only variables that were significant in at least 2 of the 9 years were selected for the full model. The reduced model included exactly two variables from each model category.

Full model

The number of years each coefficient was statistically significant, along with the range of P values, coefficient sizes, and odds ratios, is presented in Table 4. Pseudo R^2 values ranged from 0.53 to 0.72. Biophysical variables

Table 3 The number of years each variable was statistically significant ($P < 0.05$) and the range of pseudo R^2 values from stepwise logistic regression models for each category

Category (pseudo R^2 range)	Variable	Years significant (max. 9)
Supply of amenities	Campgrounds[a]	0
	Seasonal homes	3
(0.02–0.09)	Retirement counties	3
Transportation	Airports	8
(0.03–0.16)	Highways distance	7
Demand for goods[b]	Nurseries	2
	Sawmills	3
(0.09–0.28)	Household wood	8
	Christmas tree farms	2
	Gravity	5
Source infestation	Lagged distance to outbreak (1 year)[c]	8
(0.25–0.50)		
Population distribution	Distance to 1 moth per trap line	9
(0.43–0.64)	Lagged positive trap	9
	Treatment[d]	0
Ecophysical	Susceptible basal area	3
(0.22–0.51)	County latitude	9
	County longitude	9
	County area[e]	6

Variables that were significant for more than 1 year were selected in our full model (cf. Table 4), while the top two in each category were selected for our reduced model

[a] Campgrounds were included in the full model because they are likely the destination of firewood movement, have received much attention in the dispersal of invasive species and are nearly significant 4 years in the stepwise logistic regression models

[b] The number of years income and big box retailers are significant changes with demographic variables and with the gravity variable, 4–6 and 3–1 respectively

[c] Lagged distance to outbreak (4 years) was significant 6 years and size of an outbreak within 100 km, 1 and 4 year lags, was never significant. Due to concerns of multicollinearity, only lagged distance to outbreak (1 year) was included in the full and reduced model

[d] Treatment was included in the full model because it likely represents a deterrent to gypsy moth spread

[e] County area was omitted from the full model because other variables accounted for spatial dependence

that account for spatial processes of dispersal (latitude and longitude, distance to the 1 moth per trap line, and temporally lagged positive trap) were frequently significant ($P < 0.05$) with the expected signs. Two anthropogenic variables that were consistently positive and statistically significant were income and household use of wood energy ($P < 0.05$) in 5 years. Another anthropogenic variable, the number of campgrounds in the county, was positively significant in 2 years ($P < 0.05$) and nearly significant in 2 years ($P < 0.10$), while airports were positively significant once ($P < 0.05$) and nearly significant in another year ($P < 0.10$). The gravity variable was negatively significant in 2 years ($P < 0.05$) and nearly negatively significant another 2 years ($P < 0.10$). The number of sawmills was negatively significant twice ($P < 0.05$) and nearly negatively significant once ($P < 0.10$). Nurseries, and Christmas tree farms had no discernible impact. Four key results emerge from these estimation results: (1) counties with gypsy moth present in the previous year and counties closer to the population front are more likely to have gypsy moth in the subsequent year, (2) the size of the sawmill sector in the county (as a proxy for the demand for logs), likely points of transshipment, and inverse proxies for demand for imported nursery material and Christmas trees have no consistent impact, (3) counties with higher income levels have higher probabilities of gypsy moth presence, and (4) gypsy moth presence is positively related to use of household wood as a heating source.

Reduced model and model robustness

The number of years each coefficient in the reduced model is significant and the range of P values, coefficient size, and odds ratios is presented in Table 5. The reduced model also has good overall explanatory power, as judged by pseudo R^2 values. The coefficients for variables that entered both the full and reduced models had the same signs and similar statistical significance across the two specifications, suggesting that those results are robust to the precise specification. All four key results stated above are confirmed in the reduced specification. Finally, the semivariograms of Pearson χ^2 residuals (Fig. 2) confirm that including county latitude and longitude, in addition to other biophysical variables, effectively addresses concerns about spatial-autocorrelation in the trap catch data for most years. In 2001 and 2004 the reduced and full models did not perform as well as other years, perhaps reflecting the stochasticity of the biological invasion process.

Table 4 Full model results of the number of years variables were significant at $P < 0.01$ and $P < 0.05$, and nearly significant at $P < 0.10$ where +++, ++ and + indicates positive and −−−, −− and − negative significance or near-significance for the respective P values

Variable	P value									Years significant	Coefficient range	Odds ratio range (95% confidence limits)
	1999	2000	2001	2002	2003	2004	2005	2006	2007			
Supply of amenities												
Campgrounds		+++		+	++				+	4	2.35–11.38	10.44 (0.81–135.1) to >999 (0.57 to >999)
Seasonal homes										0	NA	NA
Retirement counties		−−−								1	−0.84	0.19 (0.06–0.61)
Transportation												
Airports						+			++	2	0.06–0.07	1.07 (0.99–1.15) to 1.08 (1.0–1.16)
Highway distance										0	NA	NA
Demand for goods												
Gravity	−−−			−	−				−−	4	−0.01 to 0.12	0.89 (0.82–0.95) to 0.94 (0.89–0.99)
Income	++				+++		+	+++	++	5	0.04–0.10	1.04 (1.0–1.07) to 1.11 (1.05–1.18)
Nurseries										0	NA	NA
Sawmills		−−	−	−						3	−0.11 to −0.13	0.88 (0.76–1.01) to 0.89 (0.78–1.02)
Household wood		++	+++	+++		++		++		5	1.16–2.11	3.20 (1.14–9.0) to 8.21 (2.26–29.84)
Christmas trees			+							1	5.66	287.9 (0.42 to >999)
Big box retailers				+++				+		2	0.26–0.58	1.30 (0.99–1.71) to 1.78 (1.23–2.58)
Source infestation												
Lagged distance to outbreak	−−−	−−−				−−−	−−−			4	−0.01 to −0.006	0.99 (0.98–0.99) to 0.99 (0.99)
Population distribution												
Distance to 1 moth per trap line	+	−	−−	−−−	−−−			−−−	−−−	7	−0.0006 to 0.009	0.98 (0.97–0.99) to 1.01 (0.99–1.02)
Lagged positive trap	+++	+++	+++	+++	+++	+++	+++	+++	+++	9	0.41–0.96	2.26 (1.25–4.09) to 6.78 (3.66–12.49)
Treatment						+				1	1.61	4.98 (0.97–25.55)

Table 4 continued

Variable	P value 1999	2000	2001	2002	2003	2004	2005	2006	2007	Years significant	Coefficient range	Odds ratio range (95% confidence limits)
Ecophysical												
Susceptible basal area					++		++			2	2.24–2.64	9.43 (1.04–85.67) to 13.95 (1.01–192.13)
County latitude	+++		+++	+++		+++	+++		+++	6	0.000003–0.000006	1 (1)
County longitude	+++		+++	+++		+++	+++		+++	6	0.000003–0.000008	1 (1)
County area		– –	–	–						3	−0.0036 to 0.0004	1 (1)
Pseudo R^2	0.63	0.59	0.62	0.70	0.71	0.65	0.53	0.72	0.59			

The spatial dependence of the dispersal process is highlighted by the consistently significant variables representing human population distribution. When controlling for spatial dependence, household wood, income, and campgrounds are the anthropogenic variables most often significant

Discussion

The estimation results are consistent with stratified dispersal of gypsy moth in the transition zone: variables expected to influence natural diffusive spread and variables expected to influence long-distance anthropogenic spread are statistically significant. The importance of anthropogenic factors in general is confirmed by the positive statistical significance of income.

In terms of specific invasion pathways, the most suggestive result is the positive association between the number of households that use wood as a primary source of energy and gypsy moth presence, which was statistically significant in 5 and 6 years in the full and reduced models, respectively. The corresponding odds ratios suggested that for a 1,000 unit increase in the number of homes using wood as a primary heating source, gypsy moths are 3–8 times more likely to be recorded in traps set in the county. The number of campgrounds in a county was significant twice and nearly significant twice in the full model (Table 4). Odds ratios in these years suggested at least a tenfold increase in the probability of gypsy moth with a corresponding increase in the number of campgrounds. One likely explanation for this relationship is the transport of infested firewood to those campgrounds. Additionally, the gravity variable was significant in 4 years in the full model, though consistently negative. This result was unexpected, as we had hypothesized that gypsy moth would be more likely to be introduced to counties receiving more goods and people, which in turn would have high gravity values, and indeed the bivariate correlation between the gravity variable the probability of gypsy moth is consistently positive and significant. We suspect that the negative coefficient in the multivariate model reflects an urbanization effect, for example, a lack of outdoor recreation opportunities not fully captured by the campground variable.

Firewood is commonly used in the transition zone and throughout the US. A 2007 survey of voters in sixteen Northeastern and Upper Midwest states, commissioned by the Nature Conservancy, found that more than a third of those contacted use firewood. Of those, 38% moved firewood, e.g., from home to a campsite or vacation house, or from a vacation area back to home (Nature Conservancy 2007). A third of those moving firewood reported

Table 5 Reduced model results of the number of years variables were significant at $P < 0.01$ and $P < 0.05$, and nearly significant at $P < 0.10$ where +++, ++ and + indicates positive and −−−, −− and − negative significance or near-significance for the respective P values

Variable	P value									Years significant	Coefficient range	Odds ratio range (95% confidence limits)
	1999	2000	2001	2002	2003	2004	2005	2006	2007			
Supply of amenities												
Seasonal homes	+									1	0.26	1.29 (0.97–1.73)
Retirement counties		−−−								1	−0.75	0.22 (0.07–0.67)
Transportation												
Airports						+			+++	2	0.07–0.10	1.11 (1.04–1.19) to 1.07 (0.01–1.15)
Highway distance	++							+++		2	0.003–0.004	1.00 (1.0–1.01) to 1.00 (1.00–1.01)
Demand for goods												
Gravity	−								−	2	−0.04 to 0.08	0.92 (0.88–0.97) to 0.96 (0.92–1.0)
Income	+++	+	++		+++	++	+++	+++	++	8	0.05–0.12	1.03 (0.001–1.07) to 1.13 (1.07–1.19)
Household wood		++	+++	+++		++	++	++		6	0.57–1.39	2.21 (1.04–4.69) to 4.02 (1.54–10.50)
Source infestation												
Lagged distance to outbreak	−−−	−−−				−−−	−−−			4	−0.005 to −0.01	0.99 (0.99–0.997) to 0.99 (0.99–0.99)
Population distribution												
Distance to 1 moth per trap line	+	−−−	−−−	−−−	−−−			−−−	−−−	7	−0.001 to −0.02	0.98 (0.98–0.99) to 0.99 (0.99–0.99)
Lagged positive trap	+++	+++	+++	+++	+++	+++	+++	+++	+++	9	0.47–0.97	2.55 (1.47–4.42) to 6.92 (3.79–12.65)
Ecophysical												
Susceptible basal area					++		++			2	2.29–2.66	9.90 (1.19–82.59) to 14.28 (1.17–174.22)
County latitude	+++		+++	+		++	+++		+++	6	0.000002–0.000005	1.0 (1–1)
County longitude	+++			+		+++	+++		++	5	0.000002–0.000006	1.0 (1–1)
Pseudo R^2	0.59	0.54	0.58	0.66	0.69	0.58	0.51	0.70	0.57			

The reduced model results are comparable to the full model, suggesting concerns of collinearity were appropriately addressed and that we achieved a robust model specification moving it >80 km. Additional evidence of firewood movement was reported by Haack et al. (2010) who analyzed the presence of wood borers in firewood intercepted in vehicles about to cross the Mackinac Bridge between the upper and lower peninsula of Michigan. The Nature Conservancy has also identified a need for increasing awareness about the impacts of moving firewood, finding that only one in five firewood users are aware of regulations restricting the transport of firewood, but that the vast majority would be willing to limit movement of firewood and accept stronger regulations if they were better informed about the forest health implications (Nature Conservancy 2007).

Under the gypsy moth quarantine in the US, firewood and industrial wood products, nursery stock, Christmas trees, outdoor household articles, vehicles, and mobile homes are all required to be inspected and certified before being moved from inside to outside of the quarantined area (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45-4, 2008). Variables representing the size of the commercial sectors affected by these regulations, including counts of nurseries, Christmas tree farms, and big box retailers, were rarely statistically significant in the models, perhaps due to the success of quarantine measures against the movement of gypsy moth egg masses on Christmas trees, nursery stock and other goods. We also included the number of sawmills, which could potentially purchase logs from quarantined areas. The sawmill variable was significant once and nearly significant twice in the full model but with an unexpected negative correlation with gypsy moth presence. The fact that this coefficient is not positive suggests that the sawmill sector is effectively implementing the quarantine. The fact that it is actually negative in several years may reflect the fact that counties with more sawmills are more reliant on local timber supply, which would decrease the amount of timber imported from the infested zone. It could also indicate that there is information spillover from these sawmills, which are closely monitored and more likely than private citizens to be fined for any lack of compliance with the quarantine. The movement of firewood by individuals is clearly a more challenging pathway to regulate under the federal quarantine.

Our findings add to empirical evidence that people are often dispersers of invasive species (Hodkinson and Thompson 1997; Mack et al. 2000; Suarez et al. 2001) and provide evidence of a specific mechanism, firewood, for this spread. Similar to Liebhold et al. (2006) and McCullough et al. (2006) finding that private individuals' luggage is an important pathway for the introduction of invasive species, we find that a good often transported by private individuals for their own use is associated with the spread of an invasive species. In addition to gypsy moth, this invasion pathway is potentially relevant for many other biological invaders that pose threats to North America's ecosystems, such as the woodwasp *Sirex noctilio* F., Asian longhorn beetle (*Anoplophora glabripennis* Motschulsky), and emerald ash borer (*Agrilus planipennis* Fairmaire) (Cavey et al. 1998; MacFarlane and Meyer 2005; Hoebeke et al. 2005; Koch et al. 2006). For example, in simulations of the future spread of emerald ash borer, BenDor et al. (2006) found that models including quarantine enforcement to reduce anthropogenic transport yielded much slower spread rates than models without effective quarantine.

Our results suggest that the gypsy moth quarantine has not been very effective in regulating movement by the public of relatively low value and non-industrial wood products like firewood. Movement of firewood for both recreational use and home heating use are potential concerns. Both types of firewood users need to be better understood, educated, and engaged in efforts to reduce the risk of spreading biological invaders through firewood, for example, through initiatives like the Continental Dialogue on Non-Native Forest Insects and Pests. Our results also provide a cautionary note for current efforts to expand the use of bioenergy. For example, Richter et al. (2009) proposed that advanced wood combustion projects, including at the community level, could more than double the amount of wood currently used as energy in the United States. If this becomes part of an alternative energy future, it will be critical to ensure that these wood shipments do not harbor and contribute to the spread of biological invaders.

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