



Comparison of methods for estimating the spread of a non-indigenous species

Patrick C. Tobin^{1*}, Andrew M. Liebhold¹ and E. Anderson Roberts²

¹USDA Forest Service, Northeastern Research Station, 180 Canfield Street, Morgantown, WV 26505-3180, ²Department of Entomology, Virginia Polytechnic Institute and State University, 315 Price Hall, Blacksburg, VA 24061, USA

ABSTRACT

Aim To compare different quantitative approaches for estimating rates of spread in the exotic species gypsy moth, *Lymantria dispar* L., using county-level presence/absence data and spatially extensive trapping grids.

Location USA

Methods We used county-level presence/absence records of the gypsy moth's distribution in the USA, which are available beginning in 1900, and extensive grids of pheromone-baited traps, which are available in selected areas beginning in 1981. We compared a regression approach and a boundary displacement approach for estimating gypsy moth spread based on these sources of data.

Results We observed relative congruence between methods and data sources in estimating overall rates of gypsy moth spread through time, and among regions.

Main conclusions The ability to estimate spread in exotic invasive species is a primary concern in management programmes and one for which there is a lack of information on the reliability of methods. Also, in most invading species, there is generally a lack of data to explore methods of estimating spread. Extensive data available on gypsy moth in the USA allowed for such a comparison. We show that, even with spatially crude records of presence/absence, overall rates of spread do not differ substantially from estimates obtained from the more costly deployment of extensive trapping grids. Moreover, these methods can also be applied to the general study of species distributional changes, such as range expansion or retraction, in response to climate change or other environmental effects.

Keywords

Biological invasions, gypsy moth, invasion modelling, invasive species, range expansion, spread.

*Correspondence: Patrick C. Tobin, USDA Forest Service, Northeastern Research Station, 180 Canfield Street, Morgantown, WV 26505-3180, USA.
E-mail: ptobin@fs.fed.us

INTRODUCTION

The ability to estimate and predict spread in exotic invaders is a keystone process in the development of management guidelines and policy. On detection of a new invader, key questions that often arise are which areas are susceptible to infestation; how long before populations become established in these susceptible areas; and what will be the economic and ecological impacts. Moreover, a quarantine zone is often placed around the area of a new invasion, which also serves as a zone of biological interest in which detection surveys can be made to determine the extent of the invasion. In this case, the expected rate of spread can be a critical ingredient in

determining the appropriate perimeter around an infestation. In established invaders that have not yet fully invaded all susceptible habitats, estimates of spread rates can be useful predictors in determining future boundaries of infestation. In the case of forest insect pests, for example, silvicultural interventions can often minimize the inimical effect of exotics if such tactics can be implemented prior to invasion (Gottschalk, 1993).

One obstacle in developing sound approaches to managing biological invasions is the lack of reliable methods for estimating and predicting the spread of an introduced species. One critical need is the availability of sensitive survey tools for characterization of the spatial distribution of the invading

species. But equally important are methods for interpreting data from these surveys to estimate and predict expansion. Given the importance of understanding spread in invasion ecology, we present a comparison of methods used to estimate rates of spread in the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). This invasive insect has been studied extensively, and data documenting its invasion of North America are perhaps more extensive than for any other exotic invader.

The gypsy moth is historically one of the most destructive exotic species in the USA, and has defoliated an area of > 34 million ha since, 1924 (Gypsy Moth Digest, <http://na.fs.fed.us/fhp/gm/index.shtml>). It attacks over 300 deciduous and coniferous host species (Elkinton & Liebhold, 1990), and there is ample evidence of its ecological and economic impacts (Doane & McManus, 1981; Leuschner *et al.*, 1996; Sample *et al.*, 1996; Redman & Scriber, 2000). Not surprisingly, information on and interest in gypsy moth in the USA has a long history (Forbush & Fernald, 1896; Perry, 1955; Doane & McManus, 1981; Dreistadt, 1983; Liebhold *et al.*, 1989; Reardon, 1991), beginning with the first published report of its presence in Massachusetts in 1870 (Riley & Vasey, 1870). Forbush & Fernald (1896) later described the first 'space-time' data set on gypsy moth through recounts of homeowners (cf. Liebhold & Tobin, in press), by street address and year, whose property became infested with gypsy moth following the accidental release of life stages by Léopold Trouvelot in 1868 or 1869. Efforts to eradicate the Massachusetts gypsy moth population were abandoned in 1900, and since then county records of its distribution exist from 1900, making it one of the most robust space-time data sets available on an invasive species.

While primitive pheromone traps were used in an attempt to characterize the gypsy moth's distribution as early as 1893 (Forbush & Fernald, 1896), extensive trapping data from regional trap grids are available only starting around the mid-

1980s to the present in selected areas such as central West Virginia and Virginia. However, in most areas traps were deployed beginning in the mid-1990s, primarily within a transition area that spatially separates portions of the USA that are considered to be infested with gypsy moth from those in which gypsy moth is not yet present (Decision-Support System for the Slow-the-Spread of the Gypsy Moth Project, <http://da.ento.vt.edu>; Fig. 1). Currently over 100,000 monitoring traps are placed each year across a c. 170-km-wide transition area that extends from north-eastern Minnesota to North Carolina (Tobin *et al.*, 2004; Fig. 1).

Both county-level presence/absence data and trap data can be used in the estimation of gypsy moth spread. Liebhold *et al.* (1992) used county quarantine data from 1966 to 1989, while excluding all data from Michigan, and estimated an average rate of radial spread in the north-eastern USA of 20.8 km year⁻¹. This previous study was instrumental in formulating a US Department of Agriculture gypsy moth management strategy through the 'Slow-the-Spread' (STS) Program (Sharov *et al.*, 2002; Tobin *et al.*, 2004), for which a national goal of spread was set at 10 km year⁻¹ to reflect a c. 50% reduction from the historical rate of spread (Liebhold *et al.*, 1992). Under STS, gypsy moth is monitored through a comprehensive network of pheromone-baited traps. Trap-catch data are then used to determine the type and spatial extent of site-specific treatments against isolated colonies to prevent their growth and coalescence with the gypsy moth population front.

While county-level presence/absence data provide the longest continual record of historical gypsy moth spread, the amount of detail is constrained by both the binary nature of the measurements and the coarse spatial resolution of counties. In contrast, estimation of spread rates from extensive pheromone trap grids provides more detailed information, particularly on the spatial and temporal variability in spread. Here

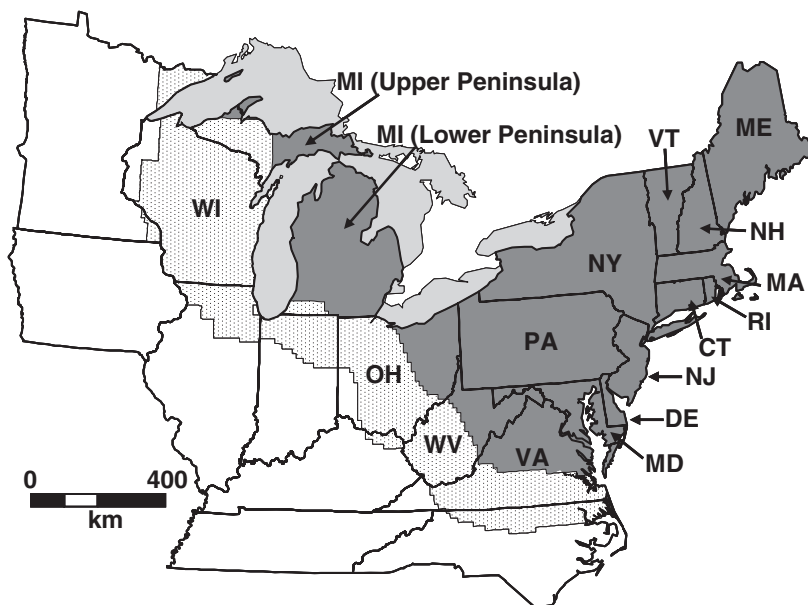


Figure 1 Map of the portions of the USA that are infested (dark grey) or uninfested (white) with gypsy moth in 2005. The dotted area between the two is the transition zone that was monitored under the STS Program in 2005. State abbreviations are also shown (see Table 1).

we extend prior work by Liebhold *et al.* (1992) by examining recent quarantine data and by a comparison with historical rates of gypsy moth spread. We also compared different approaches for estimating spread based on county-level presence/absence data (quarantine data), and pheromone trap-catch data, to show relative congruence in overall rates of spread among the approaches and between the data sources.

METHODS

Data sources

County-level quarantine records for gypsy moth are maintained by the US Department of Agriculture (US Code of Federal Regulations, Title 7, Chapter III, Section 301.45). Generally, an entire county is usually designated part of the quarantined area when established gypsy moth populations are first detected anywhere in the county. These records are updated annually and exist from 1934 to the present. From 1900 to 1934 the infested area was defined in, or determined by, various published sources (Anon., 1907a,b; Burgess, 1913, 1915, 1930; cf. Liebhold *et al.*, 1992).

Grids of pheromone traps are deployed and male moth trap-catch data are managed under the STS Program (Sharov *et al.*, 2002; Tobin *et al.*, 2004). Detailed information on STS is also available online (<http://www.gmsts.org>). These data exist from the early to mid-1980s in parts of West Virginia and Virginia, and from 1985 to 1995 in the Lower Peninsula of Michigan. Beginning in the mid-1990s, trap-catch data extend over the entire gypsy moth transition area in the USA (Fig. 1).

Trap grid intensity within this transition area depends on the expected abundance within the transition zone, because different levels of abundance require different levels of trap intensity (Sharov *et al.*, 1996b). Higher gypsy moth densities require less spatial resolution in traps because their populations tend to be established and highly spatially autocorrelated; hence unsampled locations can be estimated through geostatistical methods, such as kriging, with less sampling support than those areas in which populations are rare, lower in abundance, and consequently less spatially autocorrelated (Isaaks & Srivastava, 1989). Thus, along the distal portion of the *c.* 170-km-wide transition zone, traps are placed in a 2-km

grid while traps in areas adjacent to the generally infested area are placed 3–8 km apart (Tobin *et al.*, 2004).

Estimation of gypsy moth spread

We considered five geographical regions in which to estimate gypsy moth spread (Table 1; Fig. 2). Two of these regions were originally analysed by Liebhold *et al.* (1992), and were (1) US counties quarantined from 1900 to 1965; and (2) US counties quarantined from 1966 to 1989, excluding all Michigan counties. The other regions were (3) counties in the lower Peninsula of Michigan, which were quarantined from 1981 to 1994; (4) counties in the upper Peninsula of Michigan and Wisconsin, which were quarantined from 1994 to 2005; and (5) counties quarantined from 1990 to 2005 in central West Virginia and Virginia. This latter region represents an area in which gypsy moth management tactics have been extensively deployed from 1990 to the present (Sharov *et al.*, 1996a; Tobin *et al.*, 2004).

County quarantine records were used in all five regions to estimate rates of spread, using two approaches. The first was originally proposed by Liebhold *et al.* (1992). In this approach, the minimum distance from a fixed reference point in space (Table 1) to each quarantined county was measured. Then the average yearly radial rate of spread was estimated as the slope from least-squares regression of the minimum distance as a function of the first year of county quarantine in PROC GLM (SAS Institute, 1999) (Fig. 3). Gypsy moth spread was estimated using different fixed reference points for each region depending on the location of the initial site of introduction or the general direction of gypsy moth spread (discussed in more detail below).

The second approach involved developing a spatial time series from county quarantine records. We placed a grid consisting of a network of 2 × 2-km cells across each of the five regions. For each year of county quarantine, we scored each cell using the centre point of the cell as its spatial coordinates, as 1 or 0, where the former designation indicates that the centre of the cell was in a quarantined county while the latter indicates the reverse. This resulted in a time series of spatially referenced binary point data that were then used in a multistep process to estimate spread. First, these data were interpolated

Table 1 Regions and locations of the fixed reference point used to estimate gypsy moth rates of spread

States*, time span	Number of counties	Fixed point used in spread estimation
ME, NH, VT, MA, CT, RI, NY, 1900–65	91	Medford, MA (42.4° N, –71.1° W)
NY, PA, OH, NJ, DE, MD, VA, WV, 1966–89	212	<i>c.</i> 25 km west of Escuminac, Quebec (48.3° N, –66.8° W)
MI, Lower Peninsula, 1981–95	68	Midland, MI (43.6° N, –84.2° W)
Central WV and VA, 1989–2005	28	<i>c.</i> 34 km south of Schenectady, NY (42.5° N, –74.0° W)
MI, Upper Peninsula and WI, 1994–2005	55	Midland, MI (43.6° N, –84.2° W)
WI, 1998–2005	40	<i>c.</i> 80 km west of Ottawa, Ontario (45.4° N, –76.7° W)

*Refer to Fig. 1 for state locations. Abbreviations: CT, Connecticut; DE, Delaware; MA, Massachusetts; MD, Maryland; ME, Maine; MI, Michigan; NH, New Hampshire; NJ, New Jersey; NY, New York; OH, Ohio; PA, Pennsylvania; RI, Rhode Island; VA, Virginia; VT, Vermont; WI, Wisconsin; WV, West Virginia.

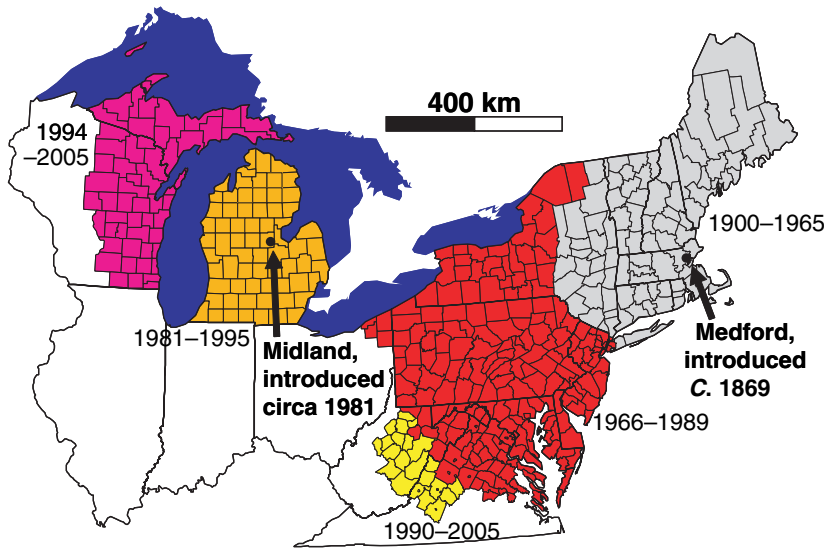


Figure 2 Counties quarantined for gypsy moth that were used in this study. (Note: this is not a complete representation of all US counties under quarantine.) Five regions were analysed separately (see Table 1). For each region, the years during which counties were quarantined are indicated. Medford and Midland are also shown as reference introduction points.

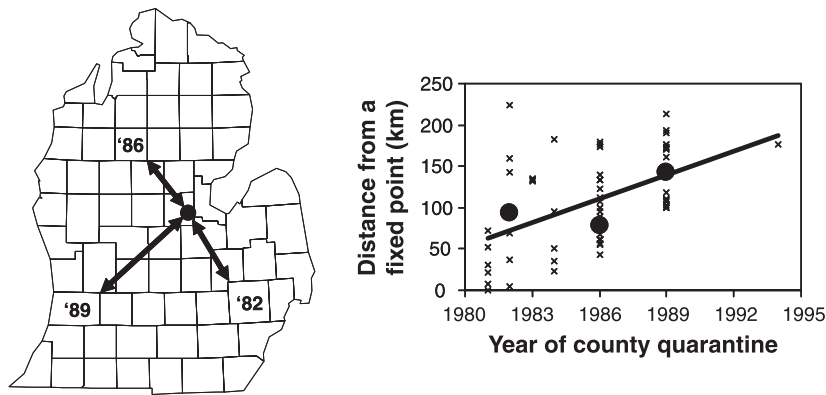


Figure 3 The least-squares regression approach to estimating rates of spread (Liebhold *et al.*, 1992). The minimum distance from a fixed point to each quarantined county, exemplified by the three highlighted counties from the map of the Lower Peninsula of Michigan, is measured and then regressed against the year of county quarantine. The scatter plot shows the regression relationship for all counties in this region, represented by crosses; closed circles represent the example counties from the map.

over a grid of 1×1 -km cells using median indicator kriging (Isaaks & Srivastava, 1989) to generate a spatially continuous surface from binary point data. Then we estimated a quarantine boundary for each year and region using an optimization algorithm (Sharov *et al.*, 1995). The distance from a fixed point in space (Table 1) to the quarantine boundary in consecutive years was measured at transects radiating from the fixed point at 0.5° intervals (Fig. 4; Sharov *et al.*, 1995). The year-to-year displacement at each transect was measured and averaged to obtain a yearly spread rate.

We also used recent pheromone trap-catch data to estimate gypsy moth spread. These data were available for three of the five regions: the Lower Peninsula of Michigan (1985–95); the Upper Peninsula of Michigan and Wisconsin (1995–2005); and central West Virginia and Virginia (1989–2005). As with the spatial time series of binary quarantine data, trap-catch data were analysed using a multistep process by first generating an

interpolated grid of 1×1 -km cells using median indicator kriging (Isaaks & Srivastava, 1989). Then we estimated population boundaries using the optimization algorithm that spatially delineated areas at which the expected catch per pheromone trap was 1, 3, 10, 30, 100 or 300 moths (Sharov *et al.*, 1995). These particular population thresholds were used because they reflected distinct population boundaries in space (Sharov *et al.*, 1997). Then we measured the distance from a fixed point in space (Table 1) to these boundaries in consecutive years at transects radiating from the fixed point at 0.5° intervals (Fig. 5; Sharov *et al.*, 1995; Tobin & Whitmire, 2005). For each population boundary we measured the year-to-year displacement at each transect, and then estimated an overall average to obtain a yearly spread rate.

To iterate, gypsy moth spread was estimated using different fixed reference points for each region (Table 1). In two of the regions, the reference point was simply the site of initial gypsy moth introduction; thus, for the region in the north-eastern

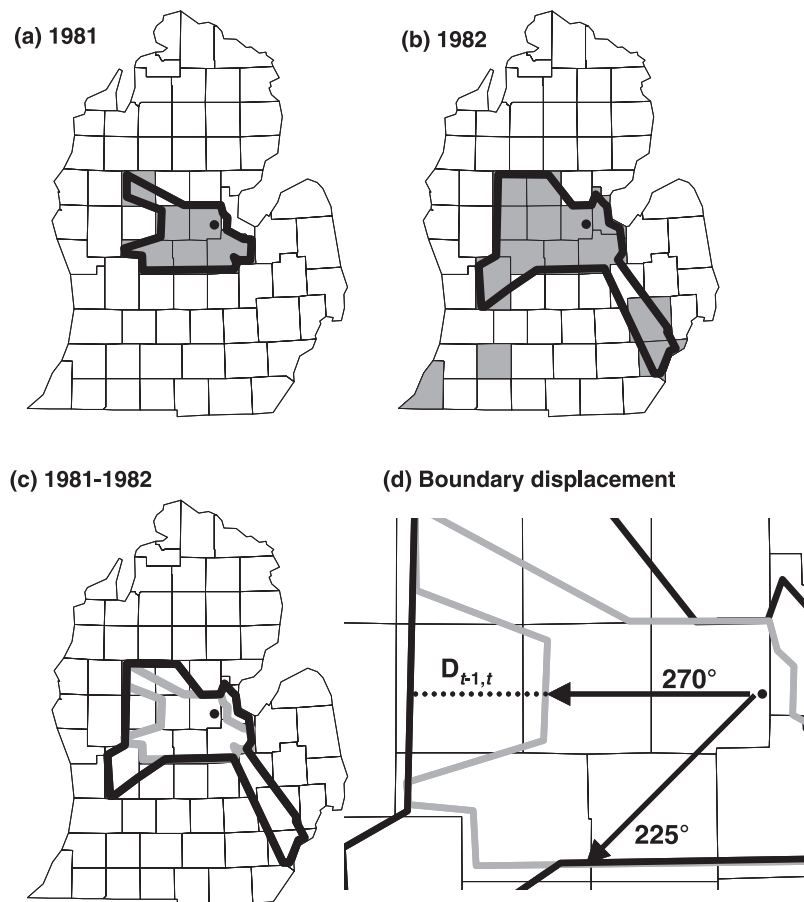


Figure 4 County-level quarantine data (shaded counties) from two consecutive years (a, b) can be used to interpolate a quarantine boundary (thick lines). The boundaries can then be compared by measuring the displacement at transects radiating from a fixed point (c). In the example in (d), the displacement at a 270° transect is $D_{t-1,t}$, while at 225° the displacement in the quarantine boundaries is 0. Displacement at all transects can be averaged to estimate the year-to-year rate of spread.

USA whose counties were quarantined from 1900 to 1965 the fixed point was Medford, MA, while for the Lower Peninsula of Michigan the fixed point was Midland, MI (Fig. 2) (Dreistadt, 1983; Tobin & Whitmire, 2005). For the other three regions the fixed point was chosen to optimize the utility of the transects, given the trajectory of gypsy moth spread (Fig. 6).

RESULTS AND DISCUSSION

The estimation of spread rates of non-indigenous species is a prime component in the development of management guidelines and policy. Because of the robust effort that has been devoted to surveying the spatial extent of invading gypsy moth populations in the USA, data from these efforts provide an ideal opportunity to explore different approaches, and the utility of different data sources, in the estimate of spread. A summary of spread rate estimates obtained from the different data sources and approaches is presented in Table 2. When applying the two approaches using county-level quarantine data, there was general congruence in the overall mean rate of spread in most of the regions, particularly when the data span several decades. The notable exception was in the Upper Peninsula of Michigan and Wisconsin (Table 2). However, one explanation could be that the trajectory of gypsy moth spread in this area occurred along opposing trajectories, which may

have provided conflicting estimates when measuring spread from a fixed point in space. Gypsy moth invaded Wisconsin from the north (from the Upper Peninsula of Michigan); at the same time gypsy moth was spreading in Wisconsin from east to west, but also from central to northern Wisconsin. When estimating spread in Wisconsin using only data from Wisconsin, estimates from both approaches were more similar (Table 2).

The availability of spatially extensive, uniformly spaced pheromone-trap grids, in which over 100,000 traps are placed annually over the transition zone between infested and uninfested areas (Tobin *et al.*, 2004), is a resource unique to the gypsy moth that is lacking in most invasive species monitoring programmes. Such robust data are likely to provide a more dependable estimate of gypsy moth spread than those estimates obtained from county-level quarantine data, which are vastly coarser. However, both sources of data provided similar estimates of spread rates over time, particularly in longer time series. The fact that presence/absence data, even on a crude spatial scale such as by county, can provide estimates close to those obtained from extensive trapping grids is encouraging for those interested in estimating distributional changes in other, less intensively monitored organisms. Moreover, this study applies not only to other invasive species programmes, but also to conservation biology. For example, understanding the change in a native species'

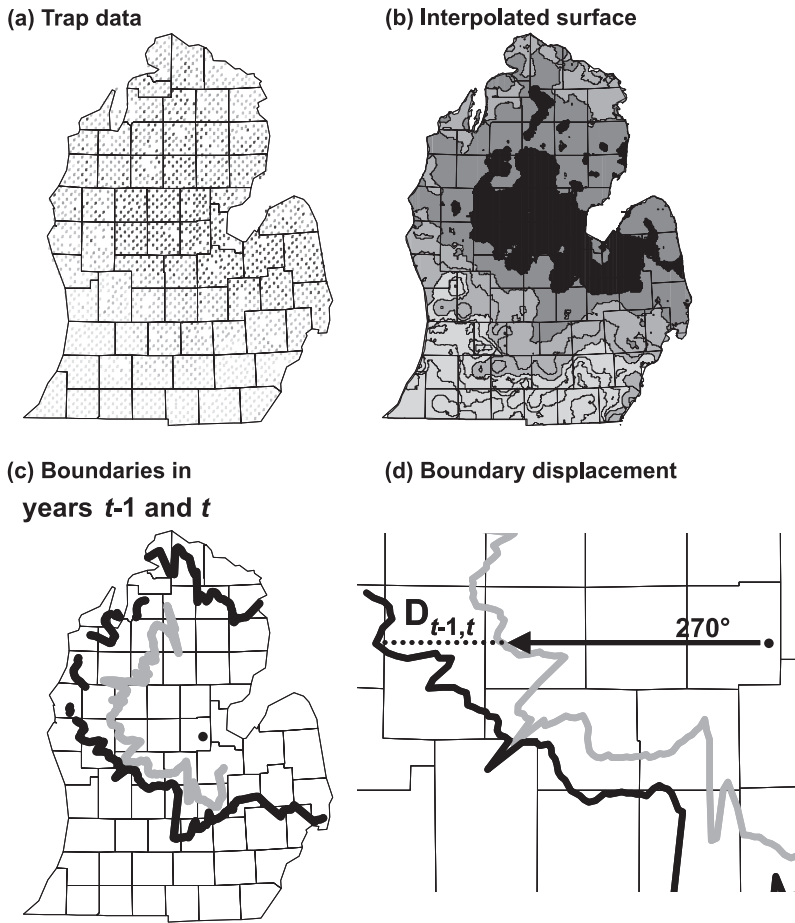


Figure 5 Gypsy moth in the USA is extensively monitored by pheromone-baited traps (a), data from which are used in geostatistical methods to interpolate abundance (b). An optimization method (Sharov *et al.*, 1995) is used to estimate population threshold boundaries (c). The displacement between thresholds from year $t - 1$ to year t is measured using radiating transects from a fixed point (d), then averaged to estimate year-to-year rates of spread.

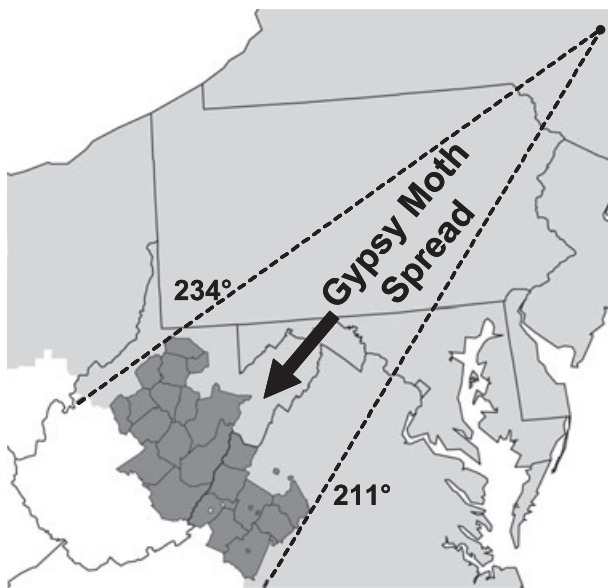


Figure 6 Selection of a fixed point in space from which to estimate gypsy moth spread rates was based on the trajectory of spread in the region of interest such that the direction of spread coincides with radii emanating from the fixed point. In central West Virginia and Virginia, this point is located about 34 km south of Schenectady, New York. In this region transects from this fixed point that were between 211° and 234° were used to measure boundary displacements.

range (Davis & Shaw, 2001; Logan *et al.*, 2003) is a parallel objective that likewise requires quantification of these changes based on survey data.

One important methodological note on the use of fixed points from which to measure spread is the precision associated with the measurement of boundary displacements. In the case of gypsy moth, transects radiating at 0.5° intervals from all fixed points (Table 1) were sufficient because there is considerable spatial autocorrelation in gypsy moth populations (Sharov *et al.*, 1996b). However, in estimating spread for populations that are spatially and temporally fragmented, more attention may be needed to ensure that transect–boundary intersections are sufficiently distributed to measure year-to-year displacements appropriately. Also, some invasion processes are dominated by stratified diffusion (cf. Shigesada *et al.*, 1995; Shigesada & Kawasaki, 1997) such that, through long-range dispersal, there is a formation of isolated colonies ahead of the general population front. The growth and coalescence of these outlying colonies with the population front can facilitate ‘jumps’ in rates of spread. Within the context of estimating spread for predictive purposes, increased variability in year-to-year boundary displacements, and non-constant rates of spread, may complicate measurements and hence require additional optimization of these approaches. However, these approaches were sufficient in estimating gypsy

Table 2 Mean (\pm SE) estimates of rates of spread (km year⁻¹) obtained from each region, across the time interval indicated, using quarantine and trap-catch data.

Region, time span	Quarantine data		Trap-catch data
	Regression method	Boundary displacement	Boundary displacement
ME, NH, VT, MA, CT, RI, NY, 1900–65	3.0 (0.3)	2.6 (1.0)	NA
NY, PA, OH, NJ, DE, MD, VA, WV, 1966–89	19.5 (0.9)	21.1 (6.3)	NA
MI, lower Peninsula, 1981–95	9.5 (1.9)	9.9 (5.0)	14.6 (3.4)
Central WV and VA, 1989–2005	7.8 (1.9)	7.6 (3.7)	5.8 (2.6)
MI, upper Peninsula, and WI, 1994–2005	28.6 (3.3)	15.9 (5.9)	18.0 (5.9)
WI only, 1998–2005	16.1 (2.2)	19.6 (6.6)	16.0 (6.1)

moth spread, which is likewise dominated by stratified diffusion (Sharov & Liebhold, 1998) and occurs at varying rates in space and time (Tobin & Whitmire, 2005).

Estimates obtained through the measurement of boundary displacements, whether the boundary delineates county-level presence/absence or moth population boundaries, would seem to provide better estimates of the variability in spread through time than the regression approach. Indeed, estimates obtained from the slope of the regression line (Table 2; Liebhold *et al.*, 1992) integrates information over a period of time to form a single estimate of radial expansion rate. In contrast, the analysis of boundary displacement allows for more detailed characterization of spread rates through space (among different radii) and time (among years). Although the analysis of the displacement of boundaries derived from county-level presence/absence data will always be constrained by the limited spatial and temporal resolution of the county data, it still provides some information on spatial and temporal variability. Although estimates of spread rate from county-level data collected over a long time should not differ substantially between the regression and boundary displacement approaches, we submit that the latter provides more extensive information about temporal and spatial variability and is therefore more desirable.

Here we explored different approaches to estimating rates of spread in the gypsy moth, one of the most extensively documented invasive species in the world. Spatially robust pheromone-trap grids certainly provide the most detailed information for characterizing spatial and temporal variability in rates of spread. However, for most non-indigenous species, such detailed survey data are not available. The results presented here indicate that records of simple presence/absence by municipality can be used to obtain comparable estimates of spread rates if the deployment of extensive trapping grids is infeasible. These approaches can also be applied to the study of distributional changes in native species from the perspective of conservation biology.

ACKNOWLEDGEMENTS

We thank Kurt Gottschalk for his comments on this manuscript. We also thank Mannin Dodd and Jiang Wu (Virginia

Polytechnic Institute and State University), Amos Ziegler (Michigan State University), and Gino Luzader and Laura Blackburn (USDA Forest Service) for their assistance in data acquisition and compilation.

REFERENCES

- Anon. (1907a) *Second annual report of the superintendent for suppressing the gypsy and brown-tail moths*. Massachusetts Public Document Number 73. Wright and Potter, Boston, MA.
- Anon. (1907b) *Report of the commissioner for the suppression of the gypsy and brown-tail moths. State of Rhode Island and Providence Plantations*. Freeman Co., Providence, RI.
- Burgess, A.F. (1913) *The dispersion of the gypsy moth*. Bulletin Number 119. US Department of Agriculture, Washington, DC.
- Burgess, A.F. (1915) *Report on the gypsy moth work in New England*. Bulletin Number 204. US Department of Agriculture, Washington, DC.
- Burgess, A.F. (1930) *The gypsy moth and the brown-tail moth*. Farmers' Bulletin 1623. US Department of Agriculture, Washington, DC.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.
- Doane, C.C. & McManus, M.E. (eds) (1981) *The gypsy moth: research toward integrated pest management*. Technical Bulletin 1584. US Department of Agriculture, Washington, DC.
- Dreistadt, S.H. (1983) An assessment of gypsy moth eradication attempts in Michigan (Lepidoptera: Lymantriidae). *Great Lakes Entomologist*, **16**, 143–148.
- Elkinton, J.S. & Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–596.
- Forbush, E.H. & Fernald, C.H. (1896) *The gypsy moth*. Wright and Potter, Boston, MA.
- Gottschalk, K.W. (1993) *Silvicultural guidelines for forest stands threatened by the gypsy moth*. General Technical Bulletin NE-171. US Department of Agriculture, Washington, DC.

- Isaaks, E.H. & Srivastava, R.M. (1989) *An introduction to applied geostatistics*. Oxford University Press, New York.
- Leuschner, W.A., Young, J.A., Walden, S.A. & Ravlin, F.W. (1996) Potential benefits of slowing the gypsy moth's spread. *Southern Journal of Applied Forestry*, **20**, 65–73.
- Liebhold, A.M. & Tobin, P.C. (in press) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. *Population Ecology*.
- Liebhold, A.M., Mastro, V. & Schaefer, P.W. (1989) Learning from the legacy of Léopold Trouvelot. *Bulletin of the Entomological Society of America*, **35**, 20–22.
- Liebhold, A.M., Halverson, J.A. & Elmes, G.A. (1992) Gypsy moth invasion in North America – a quantitative analysis. *Journal of Biogeography*, **19**, 513–520.
- Logan, J.A., Régnière, J. & Powell, J.A. (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and Environment*, **1**, 130–137.
- Perry, C.C. (1955) *Gypsy moth appraisal program and proposed plan to prevent spread of the moths*. Technical Bulletin Number 1124. US Department of Agriculture, Washington, DC.
- Reardon, R. (1991) Appalachian gypsy moth integrated pest management project. *Forestry Ecology and Management*, **39**, 107–112.
- Redman, A.M. & Scriber, J.M. (2000) Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia*, **125**, 218–228.
- Riley, C.V. & Vasey, G. (1870) Imported insects and native American insects. *American Entomologist*, **2**, 110–112.
- Sample, B.E., Butler, L., Zivkovich, C., Whitmore, R.C. & Reardon, R. (1996) Effects of *Bacillus thuringiensis* Berliner var. *kurstaki* and defoliation by the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) on native arthropods in West Virginia. *Canadian Entomologist*, **128**, 573–592.
- SAS Institute (1999) *SAS/STAT User's Guide*, Ver. 8. SAS Institute, Inc., Cary, NC.
- Sharov, A.A. & Liebhold, A.M. (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications*, **8**, 1170–1179.
- Sharov, A.A., Roberts, E.A., Liebhold, A.M. & Ravlin, F.W. (1995) Gypsy moth (Lepidoptera: Lymantriidae) spread in the central Appalachians: three methods for species boundary estimation. *Environmental Entomology*, **24**, 1529–1538.
- Sharov, A.A., Liebhold, A.M. & Roberts, E.A. (1996a) Spread of gypsy moth (Lepidoptera: Lymantriidae) in the Central Appalachians: comparison of population boundaries obtained from male moth capture, egg mass counts, and defoliation records. *Environmental Entomology*, **25**, 783–792.
- Sharov, A.A., Liebhold, A.M. & Roberts, E.A. (1996b) Spatial variation among counts of gypsy moths (Lepidoptera: Lymantriidae) in pheromone-baited traps at expanding population fronts. *Environmental Entomology*, **25**, 1312–1320.
- Sharov, A.A., Liebhold, A.M. & Roberts, E.A. (1997) Methods for monitoring the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in the Appalachian mountains. *Journal of Economic Entomology*, **90**, 1259–1266.
- Sharov, A.A., Leonard, D., Liebhold, A.M., Roberts, E.A. & Dickerson, W. (2002) 'Slow the Spread': a national program to contain the gypsy moth. *Journal of Forestry*, **100**, 30–35.
- Shigesada, N. & Kawasaki, K. (1997) *Biological invasions: theory and practice*. Oxford University Press, Oxford, UK.
- Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modeling stratified diffusion in biological invasions. *The American Naturalist*, **146**, 229–251.
- Tobin, P.C. & Whitmire, S.L. (2005) The spread of gypsy moth and its relationship to defoliation. *Environmental Entomology*, **34**, 1448–1455.
- Tobin, P.C., Sharov, A.A., Leonard, D.S., Roberts, E.A. & Liebhold, A.M. (2004) Management of the gypsy moth through a decision algorithm under the Slow the Spread Project. *American Entomologist*, **50**, 200–209.

BIOSKETCHES

Patrick C. Tobin is a research entomologist with the USDA Forest Service Northern Research Station in Morgantown, WV, USA. His primary research interests are the population biology and spatiotemporal ecology of invasive forest insects.

Andrew A. Liebhold is a research entomologist with the USDA Forest Service Northern Research Station in Morgantown, WV, USA. His primary research interests are the population biology of invasions by forest insects and the spatial dynamics of forest insect outbreaks.

E. Anderson Roberts is a Senior Research Associate in the Department of Entomology at Virginia Tech in Blacksburg, VA, USA. His primary interests are in the use of geographical information systems in integrated pest management programmes. He currently manages the southern portion of the information system for the National Slow the Spread of the Gypsy Moth Project.

Editor: Bradford Hawkins