

## Gypsy Moth (Lepidoptera: Lymantriidae) Spread in the Central Appalachians: Three Methods for Species Boundary Estimation

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**ABSTRACT** Estimation of the boundary of the geographic distribution of gypsy moth, *Lymantria dispar* (L.), populations is important for monitoring and controlling the spread of this species in North America. In this study, gypsy moth population boundaries were estimated from male moth counts in pheromone-baited traps and from egg mass counts in a 5.18-million-ha area in northwestern Virginia and southeastern West Virginia. Population boundaries were estimated for 5 yr (1988–1992) and for different population density thresholds using the following 3 methods: (1) best classification (minimizing the number of grid cell misclassifications), (2) 1st occurrence method, and (3) logistic regression of log population counts versus distance perpendicular to population boundary. All 3 methods generated similar boundaries for male moth counts, and boundaries obtained with the first 2 methods were most correlated. The regression method failed to estimate boundaries of egg mass populations because of their irregular spatial distribution. However, the 2 other methods were successful and yielded similar results. The average gypsy moth spread rate estimated using male counts was 10.7–11.9 km/yr. The minimum spread rate was 3.8–4.9 km in 1991, and the maximum rate was 19.4–22.6 km in 1989.

**KEY WORDS** *Lymantria dispar*, boundary, biological invasions, geostatistics

THE GYPSY MOTH, *Lymantria dispar* (L.), was accidentally introduced to North America near Boston in 1869 and since that time it has been slowly expanding its range (Liebhold et al. 1989, 1992). In some of the areas where this species has become established, extensive mortality of trees, destruction of wildlife habitats, and deterioration of forest aesthetic and recreational value has occurred. These effects have prompted extensive applications of pesticides in both forested and urban locations (Doane and McManus 1981). Liebhold et al. (1992) estimated gypsy moth spread rates using the relation between the date of 1st infestation and distance from the area infested in 1900. The rate of spread was relatively high (9.45 km/yr) from 1900 to 1915, in 1916–1965 it was very low (2.82 km/yr), and in 1966–1990 it increased to 20.78 km/yr in counties where the mean minimum January temperature was  $>7^{\circ}\text{C}$ .

Currently the USDA Forest Service is conducting a pilot program to evaluate the feasibility of slowing the spread of the gypsy moth in specific portions of North Carolina, Virginia, West Virginia, and Michigan (McFadden and McManus 1991, McManus and Leuschner 1995, Leonard and

Sharov 1995). To evaluate the effectiveness of this program, it is necessary to accurately measure gypsy moth spread rates in particular locations. Spread rate can be estimated as a distance between population boundaries in 2 consecutive years. Thus, the problem of population spread estimation can be reduced to the problem of population boundary estimation.

Traditionally, species boundaries have been based on qualitative 1st occurrence data (Hengeveld 1989). Boundaries are drawn by hand, connecting most distant points on the map. This method does not account for the distribution of negative observations in space, and it does not provide any measures of uncertainty.

The term *boundary* has at least 2 meanings in ecology: ecotone and isoline. An ecotone is defined as an area with the highest rate of change in population densities or ecological factors, or both (Burrough 1986, Fortin 1994). Ecotone lines are often discontinuous, and thus, they cannot be used to delineate the area occupied by a population. An isoline is a line where some ecological characteristic (for example, population density) equals a specific threshold value.

We define a population boundary as an isoline that separates areas with population density generally below and generally above a certain thresh-

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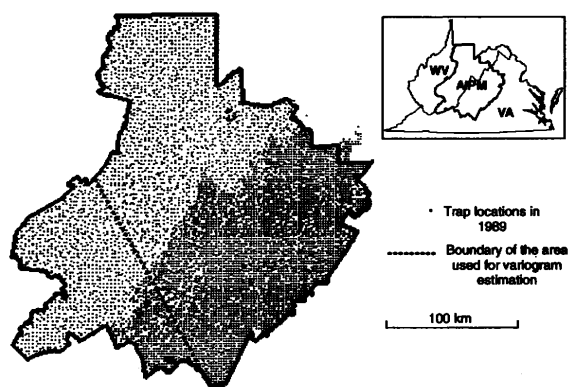


Fig. 1. Appalachian Integrated Pest Management (AIPM) area and trap locations in 1989.

old at a particular spatial scale. According to this definition, a population boundary depends on 2 criteria: threshold density and spatial scale. Threshold density is important when populations are evaluated on a continuous scale rather than as simply presence-absence. Spatial scale is important because the area occupied by a population is a fractal (Williamson and Lawton 1991, Palmer 1992) but spatial details of the fractal are only approximate at lower resolutions. When estimating gypsy moth spread rate, we were interested in a relatively large spatial scale that ignores the distinction between favorable and unfavorable habitats. Gypsy moth spreads mainly because of long-range transportation of egg masses by humans (McFadden and McManus 1991). Small patches of unfavorable habitats cannot affect its spread rate, and thus, gypsy moth spread cannot be studied at small spatial scales.

Our objectives were to develop quantitative methods for estimation of population boundaries using spatially-distributed samples, to compare boundaries of gypsy moth populations obtained by these methods, and to estimate actual gypsy moth spread rates.

#### Materials and Methods

**Area and Data.** We used historical pheromone trap data (1988–1992) and egg mass data (1988–1991) collected during the Appalachian Integrated Pest Management (AIPM) program (Reardon 1991) (Fig. 1). The objectives of the program were to demonstrate the use of new tools for minimizing the effects and the spread of the gypsy moth along its advancing front in the central Appalachians Mountains, located in portions of Virginia and West Virginia.

A grid of pheromone traps was deployed annually in 1988–1992. All traps were the standard 1.9-liter milk-carton design and were baited with (+)-disparlure impregnated dispensers (Schwalbe 1981). In Virginia, traps were placed on a  $2 \times 2$  km grid and in West Virginia a  $3 \times 3$  km grid was

used (Fig. 1). If the grid node fell on an inaccessible location (for example, a cliff) or in an unsuitable habitat for the gypsy moth (for example, an agricultural field), the trap was located in the closest suitable location within a target circle of radius 30% of the grid cell size. If no suitable location could be found, the trap was omitted. In some locations ahead of the gypsy moth infested front, traps were placed in grids of higher densities (for example,  $500 \times 500$  m grids) to delimit new populations for future eradication. In 1991 and 1992, the traps were deployed at  $6 \times 6$  km grid in the northern area where gypsy moth densities were high. The number of traps used annually within the AIPM area varied from 8,377 to 11,899.

Egg mass data were selected for analysis because the distribution of gypsy moth eggs is more aggregated than that of male moth counts (Liebhold et al. 1995). Aggregation presents certain difficulties for estimation of population boundaries, and thus, egg mass data allowed us to test the performance of our methods. Egg masses were sampled in 0.01-ha plots mostly in the area with male moth counts of 200–300 moths per trap and more. The number of plots within a 1-km<sup>2</sup> area was determined using a sequential sampling plan (Fleischer et al. 1991) and generally ranged from 4 to 10. The number of new egg masses was counted on tree boles, branches and on the ground. Because we were interested in patterns of egg mass distribution  $>1$  km, egg mass counts were averaged in each 1 km<sup>2</sup> cell before analysis.

The location of traps and egg mass samples was recorded using universal transverse mercator (UTM) (Snyder 1987) coordinates estimated from locations on standard 1:24,000 topographic maps published by the U.S. Geological Survey.

**Regular Boundaries.** We consider a population boundary as *regular* if any perpendicular to the general boundary direction, crosses the boundary only once (Fig. 2A). Actual boundaries may be highly irregular because of local complexities such as folds, *islands*, and *gaps*. An island is an isolated colony beyond the population front, and a gap is an area where populations are absent within the generally infested region (Fig. 2B). It is difficult to measure population spread by comparing actual boundaries; however, regular boundaries are easy to compare using the distance between them perpendicular to the general boundary.

We developed the following 3 methods for estimating regular population boundaries: (1) best classification of grid cells, (2) 1st occurrence method, and (3) logistic regression of log population counts versus distance perpendicular to the general boundary direction. This set of methods is not exhaustive; it only represents the history of our research. Each method evolved to the point where we felt that further improvement was not possible. The first 2 methods were based on the analysis of interpolated gypsy moth population samples. Interpolation was performed using kriging.

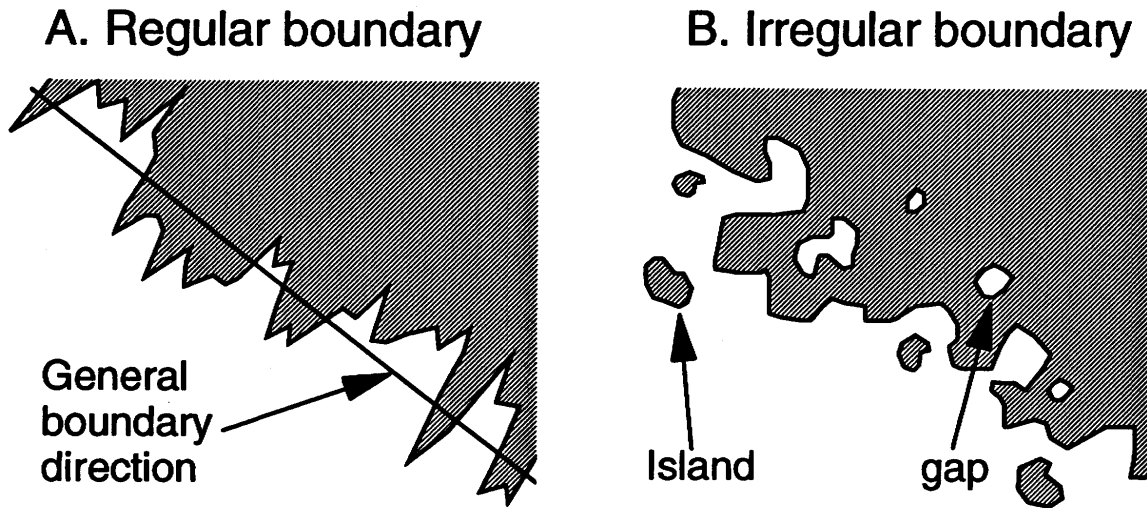


Fig. 2. Regular (A) and irregular (B) population boundaries.

**Kriging.** Kriging is a common interpolation method that was originally developed for geological problems (Isaaks and Srivastava 1989), but recently has been adopted in population ecology (Rossi et al. 1992, Liebhold et al. 1993). Kriging generates a continuous surface using weighted averages of values at nearby samples. Weights are estimated from a variogram, which represents spatial dependence among samples as a function of distance. We used median indicator kriging, which generates a continuous surface of cumulative probability that population counts are below a specified threshold (Isaaks and Srivastava 1989).

Sample indicator variograms were estimated from a data subset in the northeastern portion of the AIPM area (Fig. 1), where gypsy moth populations were detected in most samples and where all population boundaries were located. The area below the line was not used for variogram estimation because gypsy moth populations had a different spatial pattern there (scattered isolated colonies), and we needed higher kriging precision in the area above the line than below the line. Indicator variograms were estimated at median thresholds. Medians of male counts were 9, 32, 48, 41, and 23 moths per trap in 1988–1992, respectively. Medians of egg mass counts were 0, 1, 0.25, and 0 egg masses per 0.01 ha in 1988–1991. Because 0 thresholds cannot be used for estimation of indicator variograms, we used a threshold of 0.05 egg mass per 0.01 ha in 1988 and 1991.

Variograms were estimated for 4 directions (S–N, SW–NE, W–E, and NW–SE) using a 1-km lag step, 5-km band width, and 22.5° azimuth tolerance (Deutsch and Journel 1992), and an omnidirectional (all directions included) variogram was estimated. Because the variograms for different directions were similar within 15-km lag, which was the maximum interpolation distance used in krig-

ing, the omnidirectional variogram was used in kriging.

Omnidirectional variograms averaged for all years were fit with the exponential model:

$$\gamma(h) = c_0 + c_1[1 - \exp(-3h/a)] \quad (1)$$

where  $\gamma(h)$  is the variogram (that is, half the average squared difference between data points separated by lag distance  $h$ ),  $c_0$ ,  $c_1$ , and  $a$  are model parameters which are called the nugget effect, sill, and effective range, respectively (Isaaks and Srivastava 1989). The nugget effect is the variogram value at extremely small lag distances. The sill is the difference between variogram asymptotic value and the nugget effect. Effective range is the lag distance where the variogram almost reaches the sill. Parameters were estimated using a nonlinear regression procedure NLIN (SAS Institute 1992) for the points within a lag distance of 15 km. Because nonlinear regression may produce undesirable errors at small lags (Deutsch and Journel 1992), we plotted variograms to check the model fit at small lags.

Median indicator kriging was performed on a lattice of cells ( $1 \times 1$  km) using the following population thresholds: 1, 3, 10, 30, 100, and 300 moths per trap and 1, 3, 10, and 30 egg masses per 0.01 ha. The number of neighbors used to estimate each point was allowed to vary from 2 to 12. The search radius was set to 15 km; however, in most cases the data for kriging was taken within a 4- to 7-km radius. Nugget effect was excluded from the kriging model (Deutsch and Journel 1992) when kriging egg mass counts. Egg mass counts were averaged for each cell before analysis, and thus, estimated points spatially coincided with data points. If nugget effect were not excluded, then kriging would leave the original value: 0 if average

egg mass counts were below the threshold and 1 if they were above the threshold.

Kriging was performed only within the AIPM area boundary. Egg mass samples cover only a portion of the area. Thus, egg mass kriging results were accepted only if the grid cell had >2 samples in the radius of 5 km.

Cumulative probability functions for different population thresholds were checked for proper order relations. That is, cumulative probability for a higher population threshold should not be lower than that for a lower threshold. In the case of wrong order, cumulative probabilities were corrected as suggested by Deutsch and Journel (1992). Then cumulative probability functions were converted into indicator maps using the threshold probability of 0.5.

**General Boundary Direction.** Regular population boundaries are always related to the general boundary direction (Fig. 2A) which should be known prior to analysis. This direction was determined using an iterative procedure in which boundary points were estimated using some preliminary general boundary direction, and then the direction was updated using regression analysis of boundary points considered in the rotated rectangular coordinate system with the x-axis parallel to the general direction. Boundary points were estimated using the best classification method (see below), however any other method could be used as well.

The updated general boundary azimuth  $\alpha'$  (measured by degrees clockwise from north direction) was estimated as

$$\alpha' = \alpha - \arctan(b), \quad (2)$$

where  $\alpha$  is the azimuth of the initial general boundary,  $b$  is the slope of the regression of boundary points versus distance along the initial general boundary, and the arctangent is measured in degrees from  $-90$  to  $90^\circ$ . If the equation (2) yielded a value  $<0$  or  $>180^\circ$ , then  $180^\circ$  was added or subtracted from it, respectively. Updated general boundary direction was used in the next iteration, and so on. The algorithm terminated when the absolute value of the regression slope,  $b$ , became smaller than a desired accuracy level ( $10^{-4}$ ) or when the maximum number of iterations (20) was reached. In some cases, the desired level of accuracy was not reached in 20 iterations, but the slope was still acceptable if its absolute value was  $<0.005$ . This iterative regression procedure is analogous with principal component analysis, but regression was selected because the algorithm is simpler.

The general boundary directions were estimated for 5 yr and 6 moth count thresholds (that is, 30 combinations total). Results were analyzed using a 2-way analysis of variance (ANOVA) with an additive model with year and population threshold as effects. The average general boundary direction was used for estimation of regular population boundaries. It was important to use the same general

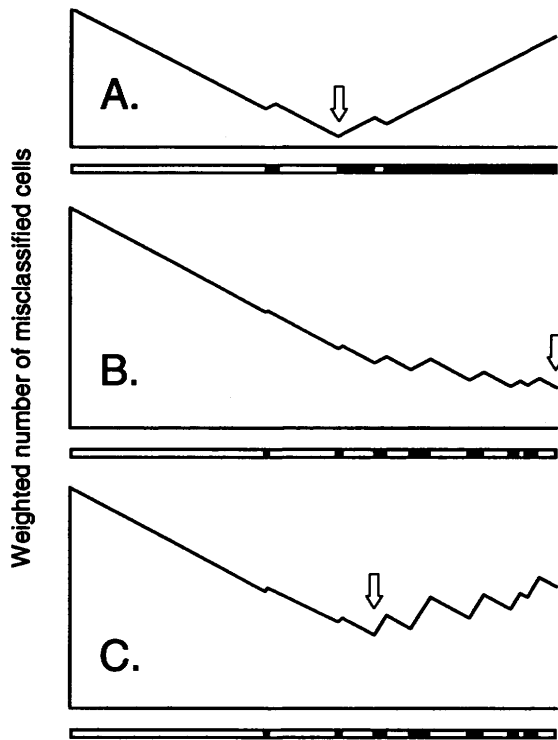
boundary direction for all estimated population boundaries because it simplified boundary comparison and gypsy moth spread rate estimation. Analysis of population boundaries is not sensitive to small variation in general boundary direction. Thus, averaging of general boundary directions could not affect the quality of our analysis.

**Best Cell Classification Method.** This is a new method that converts an indicator map into a regular population boundary. Any boundary line classifies the cells in a raster map as occupied by the population or as unoccupied. Some cells may be misclassified; for example, a cell occupied according to the indicator map can be considered as unoccupied according to the boundary line. The idea was to find the best regular population boundary that minimized the number of misclassified grid cells.

The following algorithm was used. The entire area was subdivided into 1-km-wide strips perpendicular to the general boundary direction. First, we evaluated each 1-km<sup>2</sup> cell in a strip (a cell was attributed to a strip if its center was located within the strip) and considered it as a boundary point. All the cells on one side of the location were considered as occupied, and the cells on the other side were considered as unoccupied. All misclassified cells in the strip were counted. This procedure was repeated for all cells along the strip, and the location at which the number of misclassified cells was minimal, was considered as the best boundary point (Fig. 3A). These points were connected among the strips to make a line of population boundary.

The following 2 types of cell misclassification were considered: (1) the cell is occupied but classified as unoccupied, and (2) the cell is not occupied but classified as occupied. In certain cases, the best classification method can be improved by assigning different weights to cell misclassifications of the 1st and 2nd type and minimizing the total weighted number of misclassified cells. For example, if the population distribution is patchy and the distance between patches exceeds patch size, then no boundary can be detected using equal weights for cell misclassifications of the 1st and 2nd type (Fig. 3B). The entire area will be considered unoccupied. In this case, population islands are more important for delineating a boundary than gaps. The boundary can be detected if a higher weight is assigned to the 1st type of cell misclassifications than to the 2nd type (Fig. 3C). Appropriate weights can be selected by visual comparison of actual population distribution with the estimated boundary. To get comparable boundaries, the same weights should be used in all years.

In the analysis of male moth counts we used equal weights for both types of cell misclassification, and in the analysis of egg masses we used a weight ratio of 3:1 for cell misclassifications of the 1st and 2nd type, respectively.



**Fig. 3.** Estimation of boundary points (shown by arrow) by the best cell classification method. Black regions within strips are occupied by the population, and white regions are unoccupied. The weighted number of misclassified cells within a strip reaches a minimum at the boundary point. Relative weight of misclassified occupied cells versus unoccupied cells is 1:1 (A, B) and 3:1 (C).

Boundary points located too close to the boundary of the project area are not reliable because their position can be affected significantly by population distribution outside of the project area which is unknown. Thus, we ignored boundary points located within 10-km distance (measured perpendicular to the general boundary direction) from the edge of the project area.

The number of misclassified cells has several local minima (Fig. 3), and the absolute minimum can jump from one local minimum to another when moving among the strips. Thus, the estimated boundary was erratic at 1 km resolution. To get a smooth line, we averaged boundary points in 5-km nonoverlapping intervals (Fig. 4). Boundaries were plotted in a rotated coordinate system with the x-axis parallel to the general boundary (Fig. 4). The origin of this coordinate system was selected arbitrarily so that both  $X$  and  $Y$  values were positive.

**First Occurrence Method.** An indicator roster map obtained using kriging was partitioned into strips of 1 km width perpendicular to the general boundary direction. In each strip, the 1st point from the southwest where population counts exceeded a given threshold was considered as a boundary point. The 1st occurrence method is very

sensitive to the presence of even small islands beyond the population front. Thus, population islands smaller than an arbitrarily selected minimum area (400 km<sup>2</sup> for male moths and 100 km<sup>2</sup> for egg masses) were removed. This operation is analogous to removal of outliers in statistical analysis. If the boundary point was too close to the southwest end of the strip, then it was possible that the area occupied by the population continued beyond the end of the strip. Thus, we ignored the boundary points that were located at distance <10 km from the southwest end of the strip. Boundary points were averaged in each group of 5 adjacent strips for comparison with boundaries obtained with other methods.

**Regression Method.** This method is based on the analysis of actual sample data instead of interpolated values. The entire area was partitioned into strips perpendicular to the general boundary direction, and then log-transformed population counts [ $\log_{10}(N + 1)$ ] at sampled points within a strip were regressed against the distance along the strip (Fig. 5). Strip width (5 km) was selected so that there were enough data points within each strip to perform regression analysis. These strips overlay the blocks of five 1-km strips identified for the best classification and first occurrence methods.

A nonlinear regression was used to fit a logistic model:

$$\log_{10}(N + 1) = \frac{\log_{10}(N_{\max} + 1)}{1 + \exp[-\lambda(Y - \mu)]}, \quad (3)$$

where  $N$  is population count,  $N_{\max}$  is the maximum population count,  $\lambda$  and  $\mu$  are fitted parameters, and  $Y$  is the distance along a strip, which is equal to the  $Y$  projection in the rotated coordinate system (Fig. 4).  $N_{\max}$  was kept constant (1,000 moths per trap and 200 egg masses per 0.01 ha) to avoid abnormal results in the strips with a small number of data points. A multidimensional simplex algorithm was used to minimize the residual sum of squares (Press et al. 1992). The residual sum of squares was estimated with an accuracy of  $10^{-5}$ . A regression was accepted if  $R^2 > 0.5$  and regression parameters were within the following limits:  $-200 < \mu < 200$  km,  $0.002 < \lambda < 0.2$  km<sup>-1</sup>. These limits corresponded to  $\pm 6$  SD for  $\mu$  and  $\pm 3.5$  SD for  $\lambda$  (square-root transformation was applied to  $\lambda$  to get a symmetrical distribution). The boundary point for each threshold was set at the intersection of the fitted logistic curve with that population threshold level. The boundary point was accepted if it fell within the range of primary data points in a strip. For example, if moth counts in a strip varied from 0 to 85 moths per trap, then the boundaries for moth counts of 1, 3, 10, and 30 moths per trap were accepted, and the boundaries for 100 and 300 moths per trap were excluded from further analysis.

**Comparison of Population Boundaries.** All the boundaries obtained with the 3 methods were

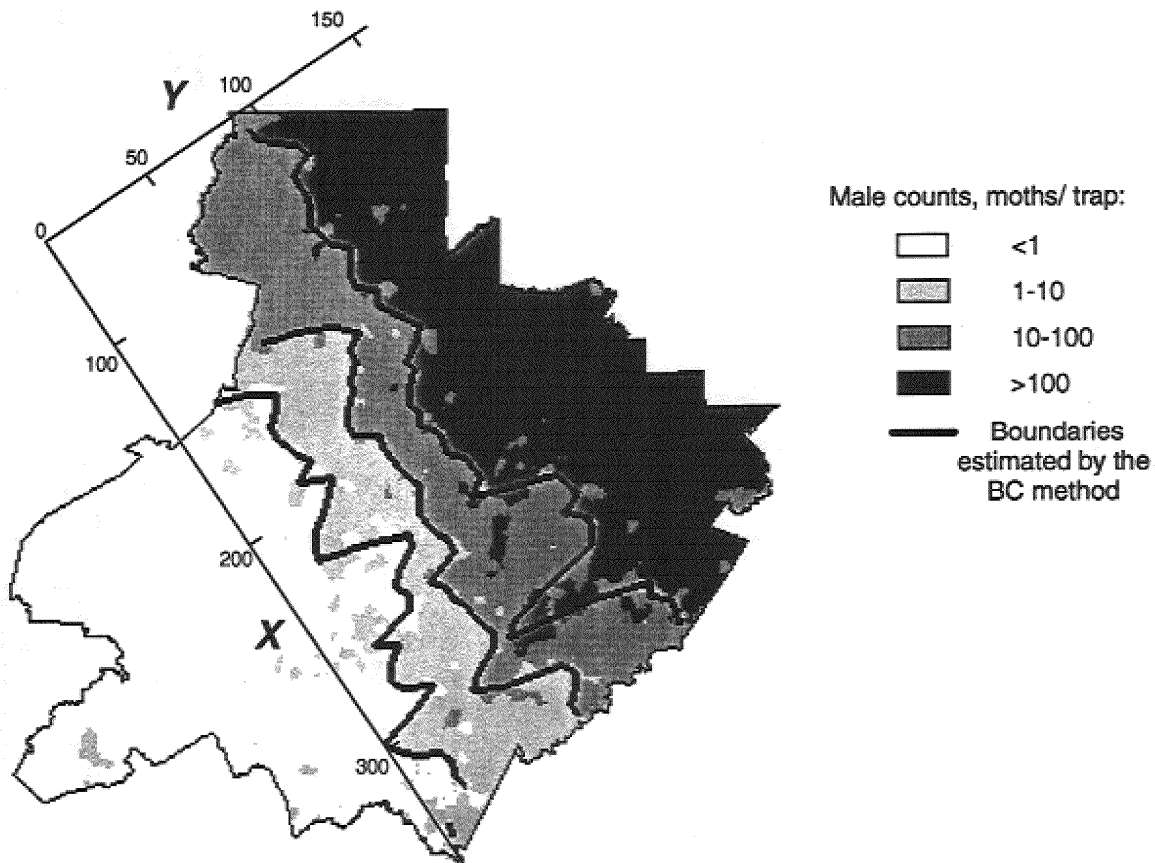


Fig. 4. Gypsy moth male counts in 1989 interpolated using indicator kriging and population boundaries for thresholds of 1, 10, and 100 moths per trap obtained using the best classification method;  $X$  and  $Y$  represent the rotated coordinate system with  $x$ -axis oriented parallel to the general boundary.

considered in the same rotated coordinate system with the  $x$ -axis oriented parallel to the general boundary. Population boundary points ( $Y$  values) were averaged within each boundary, and these av-

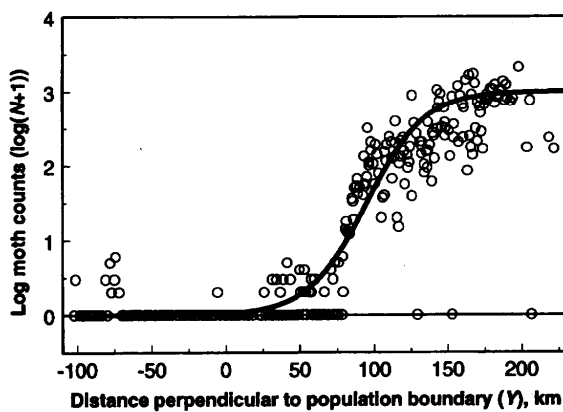


Fig. 5. Example of logistic nonlinear regression analysis of log gypsy moth male counts (males per trap) within a 5-km strip perpendicular to the general population boundary.

erages were analyzed using the general linear model (GLM) with the following 3 factors: (1) method of boundary estimation, (2) year, and (3) population threshold. Interaction of year with population threshold was incorporated into the model whereas all other interactions were considered together as an error term. Only 2 methods of boundary estimation were compared for the egg mass data because the regression method failed. An average boundary value indicates a position in the direction of population spread from northeast to southwest. The difference between average boundaries estimated with different methods was interpreted as a shift in the northeast-southwest direction.

Similarity of boundary shapes was tested using correlation among the  $Y$  coordinates of boundary points. Each pair of points was located on the same 5-km strip perpendicular to the general boundary direction. Correlation was estimated separately for each pair of methods, year, and population threshold. A general linear model was used to test the effect of the following 3 factors: (1) pair of boundary estimation methods, (2) year, and (3) population threshold on correlation among the boundaries.

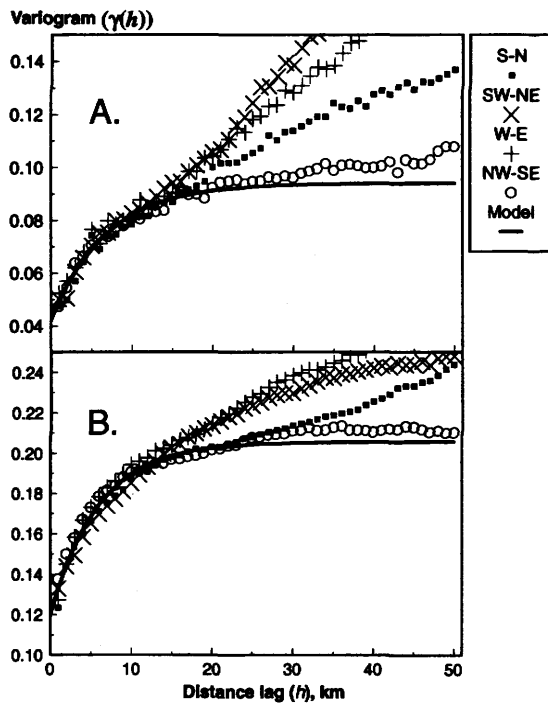


Fig. 6. Indicator variograms for gypsy moth male counts (A) and egg mass counts (B) in 4 directions and the exponential model of the omnidirectional variogram fitted within a 15-km lag range.

**Estimation of Population Spread Rate.** Population spread rate was estimated as a difference of  $Y$  projections in the rotated coordinate system between population boundaries in 2 consecutive years at 5-km intervals along the general boundary direction ( $x$ -axis). Then average spread rates obtained with each of 3 methods were analyzed for dependence on the following 2 factors: (1) year

and (2) population threshold using the 2-way ANOVA with an additive model.

**Results**

**Variograms and Kriging.** Indicator variograms for male moths and egg masses were similar in all directions at lag distance up to 15 km (Fig. 6). Beyond this distance they were different because of the trend associated with the spread of gypsy moth in the northeast-southwest direction. Variograms in the SW-NE direction, which is nearly perpendicular to the population boundary, continue increasing because of the trend whereas variograms in the NW-SE direction reach a sill.

Parameters of the exponential model fitted to sample omnidirectional variogram within 15-km lag distance were the following. For male moth counts: nugget  $c_0 = 0.042$ , sill  $c_1 = 0.052$ , and effective range  $a = 20.5$  km. For egg mass counts: nugget  $c_0 = 0.120$ , sill  $c_1 = 0.086$ , and effective range  $a = 17.8$  km. The  $R^2$  value was equal to 0.987 for male moths and 0.996 for egg masses. Visual analysis (Fig. 6) confirmed good fit. These model parameters were used for kriging. An example of kriging results taken at  $P = 0.5$  for year 1989 is shown in Fig. 4.

**General Boundary Direction.** The azimuth of the population boundary estimated by the best classification method for 5 yr and 6 thresholds of male moth counts ranged from 135.5 to 166.0° with an average of 147.5°. According to ANOVA (Table 1), it depended neither on year nor on population threshold. An azimuth of 147.5° was used as the general boundary direction for all methods of boundary estimation.

**Male Moth Boundaries.** Boundaries estimated using the best classification method roughly paralleled male moth counts isolines (Fig. 4). Bound-

Table 1. Two-factor ANOVA (additive model) of male moth population boundary azimuth and spread rate (km/yr) estimated with best classification (BC), 1st occurrence (FO), and regression (RG) methods

Factor	Factor value	Azimuth of general boundary direction	BC	FO	RG
Male count threshold (moths/trap)	1	153.4	8.9	8.1	8.3
	3	149.2	9.1	8.7	9.0
	10	146.8	9.2	9.2	11.5
	30	147.4	11.0	9.8	13.5
	100	144.4	13.6	13.5	14.3
	300	143.6	13.6	14.7	14.6
	df	5, 20	5, 15	5, 15	5, 15
	F	1.88	1.53	1.33	2.60
P	>0.05	>0.05	>0.05	>0.05	
Years	1988	151.9	—	—	—
	1989	149.4	19.6	19.4	22.6
	1990	145.1	7.2	7.5	8.8
	1991	146.0	4.9	3.9	3.8
	1992	145.1	11.9	12.0	12.3
	df	4, 20	3, 15	3, 15	3, 15
	F	1.64	19.6	11.9	33.1
P	>0.05	<0.001	<0.001	<0.001	
Grand avg		147.5	10.9	10.7	11.9

**Table 2. Analysis of population boundaries and correlations between male moth boundaries using general linear model**

Factors	Male moth boundaries			Egg mass boundaries			Correlations		
	Sum of squares	df	F	Sum of squares	df	F	Sum of squares	df	F
Method <sup>a</sup>	243	2	15	25	1	1.5NS	0.7121	2	16
Year	19,976	4	598	7,292	3	229	0.2257	4	2.5
Threshold	60,851	5	1,456	1,269	3	38	0.3514	5	3.2
Year × Threshold	1,559	20	9.3	225	9	2.5NS	—	—	—
Error	484	58	—	142	13	—	1.7303	78	—
Total	83,113	89	—	8,953	29	—	3.0195	89	—

All model effects are significant ( $P < 0.05$ ) except the 2 marked NS (not significant).

<sup>a</sup> Male boundaries were estimated by 3 methods: best classification (BC), 1st occurrence (FO), and regression (RG); egg mass boundaries were estimated by 2 methods (BC and FO); correlations were estimated for 3 method pairs (BC and FO; BC and RG; FO and RG).

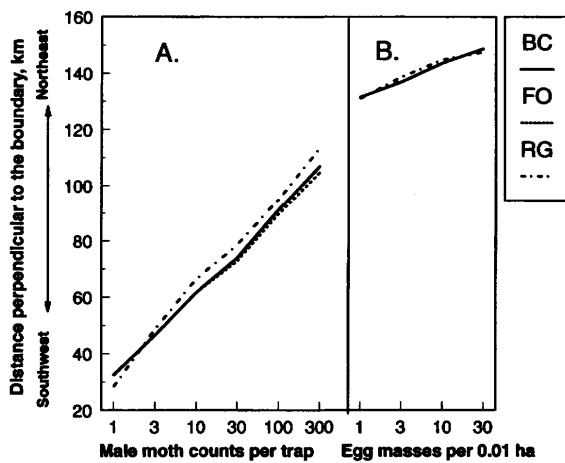
ary lines were regular: they did not include islands, gaps, or folds. In mathematical terms, they were functions in the rotated coordinate system with x-axis parallel to the general boundary direction (Fig. 4). Thus, it was possible to add, subtract, or average these boundaries.

The effect of estimation method on average male moth boundaries was significant (Table 2). Male moth boundaries estimated by the best classification and 1st occurrence methods almost coincided (Fig. 7). These boundaries were averaged twice: along the boundary and over the years. However, the regression method generated male moth boundaries for population thresholds from 10 to 300 males per trap that were shifted to the northeast by 3–9 km relative to the boundaries obtained with the 2 other methods (Fig. 7).

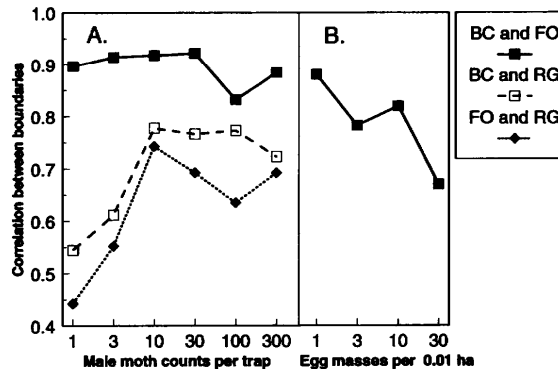
Correlation between boundaries of male moth counts estimated with the best classification and 1st occurrence methods and averaged over the years was relatively high (Fig. 8). However, bound-

aries estimated with the regression method were not well correlated with boundaries obtained with the 2 other methods. According to the general linear model analysis (Table 2), boundary correlation significantly depended on the pair of methods used for boundary estimation.

**Egg Mass Boundaries.** Analysis of egg mass population boundaries was successful with the best classification and 1st occurrence methods, but the regression method failed in the majority of strips: the  $R^2$  values were below 0.5 and corresponding boundary points were omitted causing large gaps in boundary lines (Fig. 9). In the remaining strips, the boundary was good only for the lowest threshold of 1 egg mass per 0.01 ha. For higher thresholds (for example, 10 egg masses per 0.01 ha), the boundaries did not correspond well to actual data by visual inspection (Fig. 9). Thus, egg mass boundaries obtained with the regression method were excluded from further analysis. The best classification and 1st occurrence methods failed to produce an egg mass boundary only in 1988 for population thresholds of  $\geq 3$  egg masses per 0.01 ha because the area with relatively high egg density was composed of only a few small islands.



**Fig. 7.** Location of population boundaries for different gypsy moth population thresholds (A, male moth counts; B, egg masses) estimated using best classification (BC), 1st occurrence (FO), and regression (RG) methods; boundary locations were averaged along the boundary and over the years.



**Fig. 8.** Average correlation among the boundaries (A, male moth counts; B, egg masses) obtained using best classification (BC), 1st occurrence (FO), and regression (RG) methods; correlations were averaged over the years.



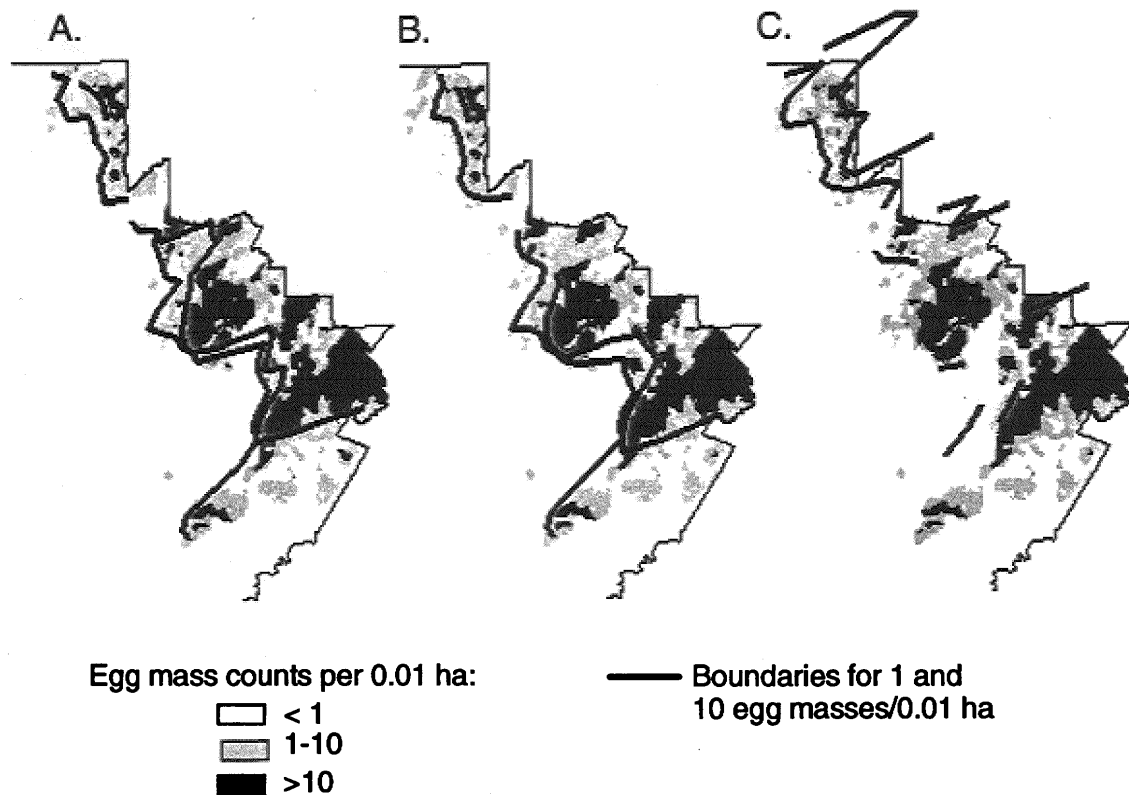


Fig. 9. Gypsy moth egg mass boundaries in 1990 estimated using best classification (A), 1st occurrence (B), and regression (C) methods.

The difference between egg mass boundaries estimated by the best classification and 1st occurrence methods was small and not significant (Fig. 7). Boundaries obtained with these methods correlated well except for 30 egg masses per 0.01 ha (Fig. 8). The highest correlation ( $r = 0.88$ ) was for the threshold of 1 egg mass per 0.01 ha, and the lowest correlation ( $r = 0.67$ ) was for 30 egg masses per 0.01 ha.

**Spread Rates.** Male moth population spread rates estimated using different methods were very close (Table 1). The grand average spread rate was estimated as 10.7–11.9 km/yr. Spread rates changed significantly from year to year (Table 1): the maximums (19.4–22.6 km/yr) were observed in 1989, and the minimums (3.8–4.9 km/yr) were observed in 1991. The pattern of spread rate change was the same for all methods of population boundary estimation (Table 1).

#### Discussion

Gypsy moth population boundaries were estimated using 2 data sets: male moth counts in pheromone traps and egg mass counts. All 3 methods tested were successful in the analysis of male moth boundaries, whereas only 2 were successful in the analysis of egg mass boundaries. The regression method appeared to be very sensitive to the type

of population spatial distribution: it failed in the analysis of gypsy moth egg masses because of their discontinuous spatial distribution with high-density patches scattered within a generally low-density area.

Several factors may be related to the low performance of the regression method. First, it was applied independently to data in each 5-km strip. Thus, local variability in egg mass density may be obscuring the population trend in some of the strips. The best classification and 1st occurrence methods were applied to interpolated data, and thus, they were less sensitive to local fluctuations. Second, the regression method is parametric, whereas the best classification and the first occurrence methods are nonparametric because they do not involve the fitting of equations. The advantage of nonparametric methods is that they are not sensitive to variable distribution, and they don't use a priori selected mathematical models.

All 3 methods yielded similar estimates of gypsy moth population spread rate in the AIPM area (Table 1). Average spread rate in 1989–1992 was 10.7–11.9 km/yr, which is  $\approx 1/2$  the spread rate in 1966–1990 (20.78 km/yr) estimated by Liebhold et al. (1992). However, 5 yr is not a long period to make a definite conclusion about the difference in spread rates. We also hypothesize that control

measures against the gypsy moth in the AIPM area might be responsible for the reduction of population spread rate since 1990.

We found great variability in the population spread rate from year to year (Table 1). According to Skellam (1951), spread rate depends on 2 factors: migration and survival-reproduction. Both factors may be quite variable from year to year. For example, survival may depend on the density fluctuations of natural enemies, especially small mammal predators (Elkinton et al. 1989). The most important factors affecting population spread are still to be identified.

Such complex phenomena as population boundary and population spread may have different formal models and different quantitative measures. Thus, we consider the proposed methods as complementary rather than alternative. When they yield similar results, then we have more confidence in their accuracy. In the same way as spatial dependence in geostatistics can be analyzed by a variety of methods (Rossi et al. 1992), the analysis of population spread will benefit from the use of different methods.

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#### References Cited

- Burroughs, P. A.** 1986. Principles of geographical information systems for land resources assessment. Clarendon, Oxford.
- Deutsch, C. V., and A. G. Journel.** 1992. GSLIB. Geostatistical software library and user's guide. Oxford University, Oxford.
- Doane, C. C., and M. L. McManus.** 1981. The gypsy moth: research toward integrated pest management. U.S. Dep. Agric. Tech. Bull. 1584.
- Elkinton, J. S., J. R. Gould, A. M. Liebhold, H. R. Smith, and W. E. Wallner.** 1989. Are gypsy moth populations in North America regulated at low density? pp. 233-249. In W. E. Wallner and K. A. McManus [eds.], *The Lymantriidae: a comparison of features of New and Old World tussock moths*. U.S. Department of Agriculture Forest Service General Technical Report NE-123, Broomal, PA.
- Fleischer, S. J., F. W. Ravlin, and R. C. Reardon.** 1991. Implementation of sequential sampling plans for gypsy moth (Lepidoptera: Lymantriidae) egg masses in eastern hardwood forests. *J. Econ. Entomol.* 84: 1100-1107.
- Fortin, M.-J.** 1994. Edge detection algorithms for two-dimensional ecological data. *Ecology* 75: 956-965.
- Hengeveld, R.** 1989. Dynamics of biological invasions. Chapman & Hall, London, New York.
- Isaaks, E. H., and R. M. Srivastava.** 1989. An introduction to applied geostatistics. Oxford University, New York.
- Leonard, D. S., and A. A. Sharov.** 1995. Slow the spread project update: developing a process for evaluation. U.S. Department of Agriculture Forest Service Technical Bulletin (in press), Radnor, PA.
- Liebhold, A., V. Mastro, and P. W. Schaefer.** 1989. Learning from the legacy of Leopold Trouvelot. *Bull. Entomol. Soc. Am.* 35: 20-21.
- Liebhold, A. M., J. A. Halverson, and G. A. Elmes.** 1992. Gypsy moth invasion in North America: a quantitative analysis. *J. Biogeogr.* 19: 513-520.
- Liebhold, A. M., R. E. Rossi, and W. P. Kemp.** 1993. Geostatistics and geographic information systems in applied insect ecology. *Annu. Rev. Entomol.* 38: 303-327.
- Liebhold, A. M., J. S. Elkinton, G. Zhou, M. E. Hohn, R. E. Rossi, G. H. Boettner, C. W. Boettner, C. Burnham, and M. L. McManus.** 1995. Regional correlation of gypsy moth (Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. *Environ. Entomol.* 24: 193-203.
- McManus, M. L., and W. A. Leuschner.** 1995. Economic evaluation of gypsy moth impacts in North America. In F. P. Hain and T. L. Payne [eds.], *Proceedings, IUFRO Conference on Forest Entomology*. U.S. Department of Agriculture General Technical Report. Radnor, PA. (in press).
- McFadden, M. W., and M. E. McManus.** 1991. An insect out of control? The potential for spread and establishment of the gypsy moth in new forest areas in the United States, pp. 172-186. In Y. N. Baranchikov, W. J. Mattson, F. P. Hain, and T. L. Payne, [eds.], *Forest insect guilds: patterns of interaction with host trees*. USDA Forest Service General Technical Report NE 153, Radnor, PA.
- Palmer, M. W.** 1992. The coexistence of species in fractal landscapes. *Am. Nat.* 139: 375-397.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery.** 1992. Numerical recipes in C. The art of scientific computing, 2nd ed. Cambridge University Press, Cambridge.
- Reardon, R. C.** 1991. Appalachian gypsy moth integrated pest-management project. *For. Ecol. Manage.* 39: 107-112.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz.** 1992. Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecol. Monogr.* 62: 277-314.
- SAS Institute.** 1992. SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Cary, NC.
- Schwalbe, C. P.** 1981. Disparlure-baited traps for survey and detection, pp. 542-548. In C. C. Doane and M. L. McManus [eds.], *The gypsy moth: research toward integrated pest management*. U.S. Dep. Agric. Tech. Bull. 1584.
- Skellam, J. G.** 1951. Random dispersal in theoretical populations. *Biometrika* 38: 196-218.
- Snyder, J. P.** 1987. Map projections—a working manual. U.S. Geol. Surv. Prof. Pap. 1395.
- Williamson, M. H., and J. H. Lawton.** 1991. Fractal geometry of ecological habitats, pp. 69-86. In S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], *Habitat structure: the physical arrangement of objects in space*. Chapman & Hall, New York.

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