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What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility?

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Abstract

1 The effect of winter temperature and forest susceptibility on the rate of gypsy moth *Lymantria dispar* (L.) range expansion in the lower peninsula of Michigan was analysed using historical data on moth counts in a grid of pheromone-baited traps collected from 1985 to 1994 by the Michigan Department of Agriculture. The rate of spread was measured by the distance between population boundaries in consecutive years. Boundaries were estimated for population thresholds of 1, 3, 10, 30, and 100 moths per trap using a polar coordinate system.

2 The average rate of spread estimated using all population thresholds was 15.8 km/yr.

3 The rate of spread was higher in the northern part of the lower peninsula than in the southern part, despite lower minimum January temperatures in the north.

4 The rate of spread was positively correlated with forest susceptibility, which was higher in the north than in the south.

Keywords Biological invasions, forest susceptibility, *Lymantria dispar*, population spread, temperature.

Introduction

The gypsy moth *Lymantria dispar* (L.), a polyphagous forest pest insect, has expanded its range in North America to the south, west and north from Boston, Massachusetts, where it was introduced in 1869. The expanding population front of the continuously infested area in the U.S.A. currently extends through Ohio, West Virginia, Virginia, and north-eastern North Carolina. Michigan apparently was colonized by the inadvertent transportation of egg masses or other life stages by humans. Isolated infestations in Michigan were first reported in the 1950s and 1960s (Dreistadt & Weber, 1989; Pijanowski *et al*., 1995). Eradication programs were conducted in these areas and they were considered successful. However, when a more attractive pheromone was identified, synthesized and included in pheromone-baited traps in 1973, gypsy moth was captured in 21 counties (Dreistadt, 1983; Dreistadt & Weber, 1989; Witter *et al*., 1992). Pesticide applications in the following years were not successful in eradicating the gypsy moth, probably because the area infested was already too large.

Studying the rate of spread of invading gypsy moth populations is important for predicting potential impacts on forests in the future (Liebhold *et al*., 1992) and for evaluating strategies for slowing its spread (Leonard & Sharov, 1995). Slowing the rate of spread postpones negative impacts on ecosystems in areas located beyond the expanding population front. A pilot project, Slow-the-Spread (STS), was initiated by the USDA Forest Service in 1993 to determine the feasibility of slowing the rate of gypsy moth spread in portions of Virginia, West Virginia, North Carolina and in the upper peninsula of Michigan (Leonard & Sharov, 1995). The general STS strategy is to detect isolated low-density colonies located just ahead of the population front, delimit their spatial extent, and employ environmentally sound suppression techniques. Sharov *et al*. (1996, 1997) showed that the rate of gypsy moth spread has declined in the Appalachian Mountains following the initiation of this programme. To expand this strategy to other geographical areas, we need more information on the factors affecting the rate of spread.

Liebhold *et al*. (1992) analysed the rate of gypsy moth spread derived from records of the time when domestic quarantine regulations were established in counties located at various distances from the initial point of introduction in North America (Boston, MA). Liebhold *et al*. (1992) did not use data from

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Michigan because their method could not be applied to secondary introductions. They found that, from 1965 to 1990, the rate of spread was much greater (20.78 km/yr) in the areas where the mean minimum January temperature was greater than – 13.8°C than in areas with a mean minimum January temperature less than – 13.8°C (7.61 km/yr). Liebhold *et al.* (1992) hypothesized that winter temperatures might be limiting the rate of population spread. Low winter temperatures occasionally caused high mortality in overwintering gypsy moth eggs (Bess, 1961; Leonard, 1972), especially in egg masses located above the snow cover level (Leonard, 1972). Increased winter mortality could be one of the mechanisms that has caused a lower rate of population spread in northern areas.

Another factor that may affect the rate of spread is habitat quality. Our preliminary analysis of moth count data from the eastern region of Virginia suggests that the rate of spread in the coastal plain is much slower than in the Appalachian mountains (unpublished data). This difference may be attributed to a lower density of host trees and a higher fragmentation of forests in the coastal plain than in the mountains.

We were interested in comparing the effect of winter temperature and habitat quality on the rate of gypsy moth spread. In this article we study the effect of these two factors in the lower peninsula of Michigan. This area was selected because of the following: (1) the area of the state is diverse in habitat quality for the gypsy moth and in climate; (2) the habitat quality generally increases to the north whereas winter temperature decreases to the north; because these factors vary in opposite directions in space, it is easy to separate their effects on the rate of spread; and (3) extensive data on male moth captures in pheromone traps were collected in Michigan beginning in 1985 (Gage *et al.*, 1990).

Methods

Data

Data on moth counts in pheromone traps in 1985–1994 were obtained from the Michigan Department of Agriculture statewide gypsy moth monitoring programme. In this programme, pheromone traps were set in grids at > 3000 permanent sites (Gage *et al.*, 1990). We used data for the lower peninsula only, because the width of the upper peninsula is not sufficient for a reliable analysis. Traps were set in a grid with the intertrap distance of ≈6.8 km. All traps were USDA milk carton traps with (+)-disparlure impregnated dispensers (Schwalbe, 1981). Traps were deployed in early July and collected in September of each year. Trap locations and moth counts were stored in a GIS (Gage *et al.*, 1990).

To relate spread rates with forest susceptibility (which we consider synonymous to habitat quality), we used a map of forest susceptibility, by county, developed by Liebhold *et al.* (1997) from forest inventory and analysis data. These authors identified 20 tree species preferred by the gypsy moth using the classification of Montgomery (1991) which was based on a summary of field and laboratory studies, as well as extrapolations based on taxonomic affinity. Preferred tree species used by Liebhold *et al.* (1997) included 13 species of oaks (*Quercus* spp.), two aspen species (*Populus* spp.), sweetgum (*Liquidambar styraciflua*), paper birch (*Betula papyrifera*), western larch (*Larix occidentalis*) and tanoak (*Lithocarpus densiflorus*). This classification does not consider the vulnerability of forest stands to damage caused by gypsy moths, which is discussed by Witter *et al.* (1992).

In Michigan, the gypsy moth feeds mostly on oaks, aspens and paper birch (Stoyenoff *et al.*, 1994), which are all considered as susceptible species by Liebhold *et al.* (1997). Aspen-fed larvae reach greater biomass at pupation than oak-fed larvae, but the survival of aspen-fed larvae is lower (Stoyenoff *et al.*, 1994).

Liebhold *et al.* (1997) estimated the following quantitative characteristics of forest susceptibility in each county: basal area of preferred species per acre, the proportion of basal area in preferred species, and the percentage land area that has > 20, 50 and 80% of tree basal area in preferred species. Because these characteristics were highly correlated, we selected only one characteristic for our analysis, which is the percentage land area that has > 50% of tree basal area in preferred species. Although this characteristic represents the quality of the habitat well, it describes habitat fragmentation only partially. Obviously, habitats are likely to be more fragmented in the region that has 10% area covered with susceptible stands than the region that has 80% area covered with susceptible stands. But the size of habitat patches is not represented in this characteristic. For example, if 10% of an area is covered with susceptible stands, then these stands can form numerous small patches, or they may be clumped into a smaller number of larger patches.

Comprehensive analysis of the effect of the size of habitat patches on the rate of population spread would require high-resolution vegetation maps that specify accurately tree species composition. However, existing maps either have a low spatial resolution or they are not sufficiently detailed in characterizing tree species. For example, the U.S. Geological Survey land use and land cover map (U.S. Geological Survey, 1986) has a relatively high resolution (250 m) but it specifies only broad forest type categories. Each of these forest types may include both susceptible and resistant trees for the gypsy moth. The proportion of these tree species may vary from region to region but the map does not capture these changes. Thus, in this paper we did not analyse effects of patch size on the rate of gypsy moth spread due to the lack of adequate data.

Temperature data from 35 weather stations scattered over the entire lower peninsula of Michigan were extracted from the U.S. National Climatic Data Center's TC-3200 Summary of the Day Cooperative Observer Network database (EarthInfo Inc., Boulder, CO). We assumed that daily minima of temperature would be more likely to affect the survival of gypsy moth eggs than daily averages or maxima. Minimum temperatures were averaged for all days in January for each year from 1986 to 1994 individually. We think that this characteristic is better than the absolute minimum temperature for the entire winter. Absolute minimum represents the coldest day, but mortality of gypsy moth eggs depends on both temperature and the duration of chilling (Madrid & Stewart, 1981). Thus, a single cold day may not be harmful.

Average minimum January temperatures were interpolated for each year in a 2-km grid using ordinary kriging with latitude as a trend variable and elevation as external drift (Deutsch &

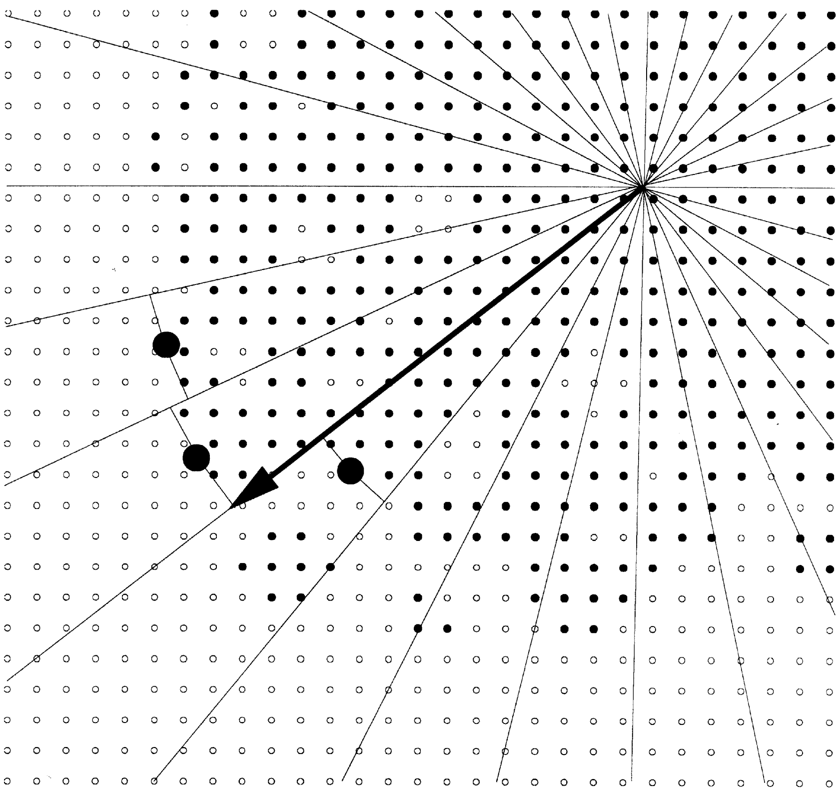

Figure 1 Delineating population boundaries using the best cell classification method in polar coordinates. A grid of cells is shown by small circles: solid circles indicate sites that have population numbers above a threshold *T*, and empty circles indicate sites with population numbers < *T*. Shaded circles correspond to boundary points; they are set at such a radius (shown by an arrow) that the number of misclassified grid cells within each sector is minimal.

Journel, 1992). Elevation data were obtained from U.S. Geological Survey 1 : 250 000 Digital Elevation Models (Elassal & Caruso, 1983).

Estimating rates of spread

The rate of population expansion was estimated as the distance between population boundaries for the same population threshold in two consecutive years (Sharov *et al.*, 1995). To determine boundaries, moth counts were interpolated in a 1 × 1 km grid using median indicator kriging with subsequent E-type estimation (Deutsch & Journel, 1992). This method provides unbiased interpolated values even if the distribution of the variable is not normal. Population thresholds $T = 1, 3, 10, 30$ and 100 moths per trap were used to estimate boundaries. Higher thresholds were not used in the analysis because these population boundaries could not be estimated in some years when moth counts were generally low.

The best cell classification method (Sharov *et al.*, 1995) was used to estimate 'regular' population boundaries. A boundary is considered regular if it has no 'islands', 'gaps', or 'folds'. If a grid of cells is applied to the area, then a boundary line classifies the cells at one side of the line as having population numbers above threshold, *T*, and the cells at the other side as having population numbers < *T*. The best cell classification method determines the regular boundary that minimizes the number of grid cells that are misclassified. Sharov *et al.* (1995) suggested separating the area into thin strips that are perpendicular to the general direction of the population boundary and minimizing the number of misclassified cells in each strip individually. In Michigan, gypsy moth populations expanded in all directions. Thus, we modified our method by using thin sectors instead of strips (Fig. 1). If the boundary line intersects a sector at radius, *r*, then cells within this sector are misclassified if they are either located at distance > *r* from the centre and have population numbers > *T*, or located at distance < *r* from the centre and have population numbers < *T*. The radius, *r*, that corresponds to the minimum number of misclassified cells is considered a population boundary point. Data analysis indicated that the population had been spreading in all directions from Midland, Michigan (Gage & Pijanowski, 1993). Thus, we set the centre of the polar coordinate system to Midland. The angle of sectors was 2°.

Population spread can not be traced beyond state borders or land surface; thus, boundary points were not used in further analysis if they were located < 15 km from the state border. Our method for estimating boundaries can not be used if the boundary is located too close to the centre (Midland, Michigan), because sectors become so thin that the number of grid cells that fit into a sector is not sufficient for estimation (Fig. 1). The minimum distance from the centre at which boundaries can be estimated equals the radius, *r*, at which the width of a sector is equal to the distance between grid nodes, *d*: $r = 0.5d/\tan(\alpha/2)$, where α is the angle of the sector. We used $\alpha = 2°$, and $d = 1$ km. Thus, $r = 28.6$ km. Boundary points located at a distance < 28.6 km from the centre were not used in further analysis.

In 1985, moth counts reported from Clinton and Ionia counties were mostly zeroes, whereas in the neighbouring counties (Shiawassee, Gratiot, and Montcalm) moth counts were > 10

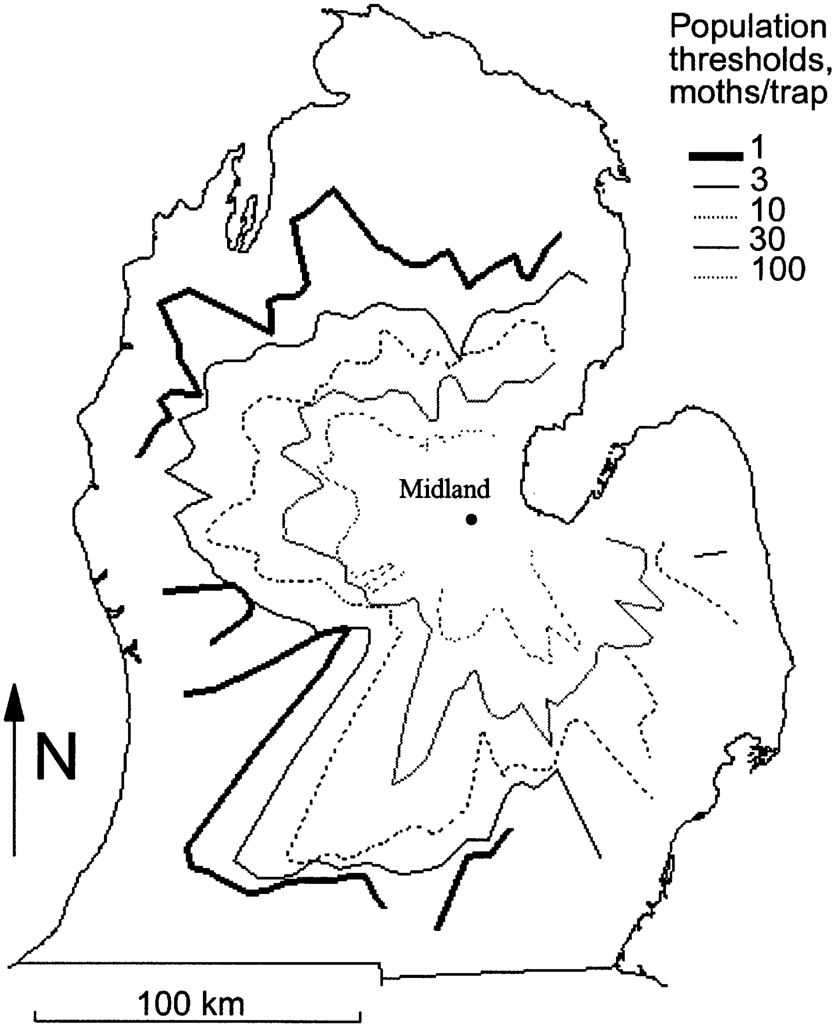

Figure 2 Population boundaries of the gypsy moth in the lower peninsula of Michigan in 1986.

moths per trap. The boundary of zero moth counts coincided with county boundaries, which possibly indicates an error in data collection. We considered data from Clinton and Ionia counties in 1985 to be suspicious and excluded population boundaries located in that area from further analysis (boundaries for 1, 3 and 10 moths per trap, azimuth from 189 to 235°).

The rate of spread was estimated for each azimuth (in 2° intervals) for each population threshold as the distance between population boundaries at consecutive years. The value of the rate of spread was considered missing if at least one boundary point was undetermined at that azimuth.

Analysis of spread rates

Means and standard deviations of spread rates were calculated for each year and population threshold using all azimuths as replications. To determine the relationship between the rate of population spread and other variables (forest susceptibility, temperature, and latitude) we combined estimates of spread rate for all years and population thresholds ($N = 2397$). For each estimate of the rate of spread we determined forest susceptibility, winter temperature and latitude at the same geographical location. Because the rate of spread is estimated as the distance between two boundary locations, we determined forest susceptibility, winter temperature and latitude in these two locations and then took the average for these locations. To study the effect of forest susceptibility, we sorted all data (pairs of the rate of spread and forest susceptibility) by increasing forest susceptibility and then subdivided them into ten classes of almost equal size. The first class had 240 data points with the lowest forest susceptibility, the second class had the next 240 data points and so on. Grouping data into classes was necessary because of high variability of spread rates. The average spread rate in each class was plotted against average forest susceptibility in the same class. The same method was used to analyse the effect of temperature and latitude.

Both the rate of spread and forest susceptibility are spatially autocorrelated variables. Thus, the significance of correlation between these variables cannot be determined using the standard *t*- or *F*-distribution. We used the method of Clifford *et al.* (1989) to determine significance. The spatial location of each data pair

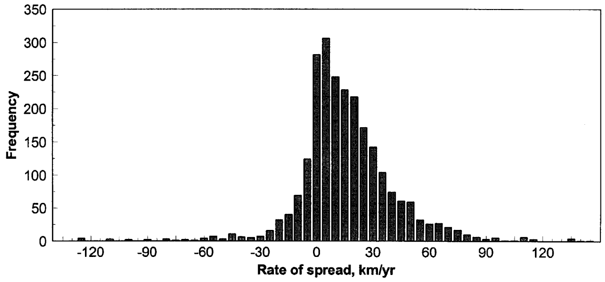

Figure 3 Frequency distribution of the local rate of gypsy moth spread in Michigan combined for all years and population thresholds.

Table 1 The rate of gypsy moth spread in the lower peninsula of Michigan estimated using various population thresholds.

Population threshold (moths per trap)	No. of estimates of spread rate	Average spread rate (km/yr)	SD of spread rate (km/yr)
1	193	15.0	27.7
3	371	15.0	22.5
10	518	15.4	21.3
30	682	16.8	29.4
100	633	15.8	24.9
All	2397	15.8	25.4

(the rate of spread and forest susceptibility) was assumed to be in the middle of the segment between the initial and final locations of the population boundary that were used for estimating the rate of spread. We used GSLIB software (Deutsch & Journel, 1992) to estimate correlograms for both the rate of spread and forest susceptibility. A correlogram, $\rho(h)$, equals the correlation in values of the variable measured in locations separated by varying distances, h (Isaaks & Srivastava, 1989). Correlograms were fitted to the exponential model:

$$\rho(h) = c \cdot \exp\left(-\frac{3h}{a}\right), \qquad \mathrm{h} > 0; \tag{1}$$

where c is the sill, and a is the range. The nonlinear regression (least square method) was used to estimate parameters c and a from sample correlograms. In the Appalachian Mountains, spread rates of the gypsy moth were correlated in space but not in time (Sharov *et al.*, 1997). Thus, autocorrelation among spread rates was considered only within the same year.

The standard error for the correlation between the rate of spread and forest susceptibility was estimated using the equation of Clifford *et al.* (1989):

$$SE_r = \sqrt{\sum_h w_h \rho_v(h) \rho_f(h)}, \tag{2}$$

where $\rho_v(h)$ and $\rho_f(h)$ are model correlograms (1) for the rate of spread and forest susceptibility, respectively, and w_h is the weight that is equal to the proportion of ordered pairs of data locations separated by distance h. Note that each pair of non-coinciding locations is counted twice for estimating weights w_h. The sum in eqn 2 includes pairs of coinciding data locations ($h = 0$) for which the correlation is equal to 1. The number of these pairs is equal to the number of data locations, N, and their proportion among all pairs of data locations is $1/N$. Thus, it is convenient to rewrite eqn 2 as

$$SE_r = \sqrt{\frac{1}{N} + \sum_{h>0} w_h \rho_v(h) \rho_f(h)}. \tag{3}$$

The effective sample size, N^*, is

$$N* = 1 + SE_r{}^{-2} \tag{4}$$

(Clifford *et al.*, 1989). The probability, P, that the null-hypothesis is true (no relationship) was then determined using the standard one-tail t-distribution with ($N^* - 2$) degrees of freedom. We used the one-tail distribution because we did not expect a negative effect of forest susceptibility on the rate of spread.

Results

Examples of population boundaries estimated for 1986 in Michigan are shown in Fig. 2. Local rates of population spread in Michigan in 1985–1993 varied from −125 to 145 km/yr, but most estimates were in the range from −30 to 85 km/yr (Fig. 3). The average rate of spread was 15.8 km/yr and the SD = 25.4 km/yr. Average rates of spread estimated using various population thresholds were very close, but SD were slightly different (Table 1). Rates estimated using the thresholds of three and ten moths per trap were least variable, and rates estimated using thresholds of one and 30 moths per trap were most variable.

Annual rates of population spread were similar for all thresholds except for 30 and 100 moths per trap in 1991–1992 (Fig. 4). Large fluctuations in the rate of spread detected using thresholds of 30 and 100 moths per trap were caused by the decline of gypsy moth numbers in 1992. As a result, population boundaries retreated. By the next year (1993) they advanced even further that the 1991 position.

The average minimum January temperature increased generally from North to South in the lower peninsula of Michigan (Fig. 5A). Forest susceptibility increased in the opposite direction from South to North (Fig. 5B). Forests in the North are susceptible to the gypsy moth largely due to the abundance of aspen. The relatively low percentage area with susceptible forests in southern Michigan (Fig. 5B) is the result of agricultural land use. Susceptible oak-dominated forests are present there, but they are fragmented and occupy a relatively small percentage of land area.

The rates of population spread increased with increasing forest susceptibility (Fig. 6A). The regression equation ($y = 10.5 + 0.408x$, $R^2 = 0.69$) is used for visual analysis only. Because data points may be autocorrelated, the significance of this relationship can not be determined from the regression. Instead, we use the method of Clifford *et al.* (1989) (see below). The rates of population spread decreased with increasing average minimum January temperature ($y = 5.3–1.17x$, $R^2 = 0.43$; Fig. 6B). Spread rates in the northern portion of the lower peninsula of Michigan were higher than in the southern portion even though winter temperatures were lower in the north than in the south (Figs 5 and 7). But both forest susceptibility and spread rates increased in a similar fashion with increasing latitude (Fig. 7).

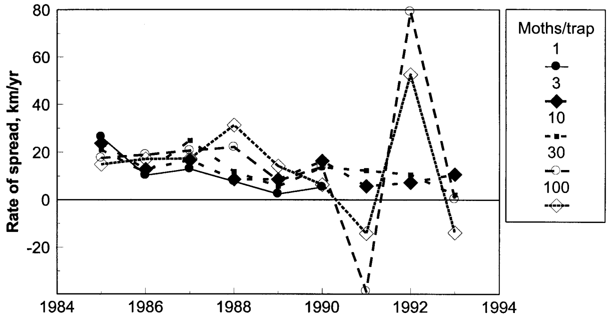

Figure 4 Dynamics of the rate of gypsy moth spread in Michigan estimated using various population thresholds.

To apply the method of Clifford *et al.* (1989) for testing the significance of the relationship between the rate of spread and forest susceptibility, we estimated correlograms for both variables (Fig. 8). Non-linear regression (1) yielded the following parameters for correlogram models: the sill in both correlograms was $c = 1$, and the ranges were $a = 113$ km for the rate of spread and $a = 315$ km for forest susceptibility. Equations (3) and (4) gave $SE_r = 0.114$ and $N^* = 78$.

The correlation between spread rate and forest susceptibility was $r = 0.185$. The t-ratio was 1.68 which corresponds to a probability of $P = 0.049$ (one-tail t-distribution). If the 11 highest estimates of the spread rates (> 110 km/yr) are considered outliers, then the t-ratio becomes 1.83 and the error probability reduces to $P = 0.036$. This indicates that the rate of gypsy moth spread in Michigan is significantly correlated with the percentage of land area occupied by susceptible forests.

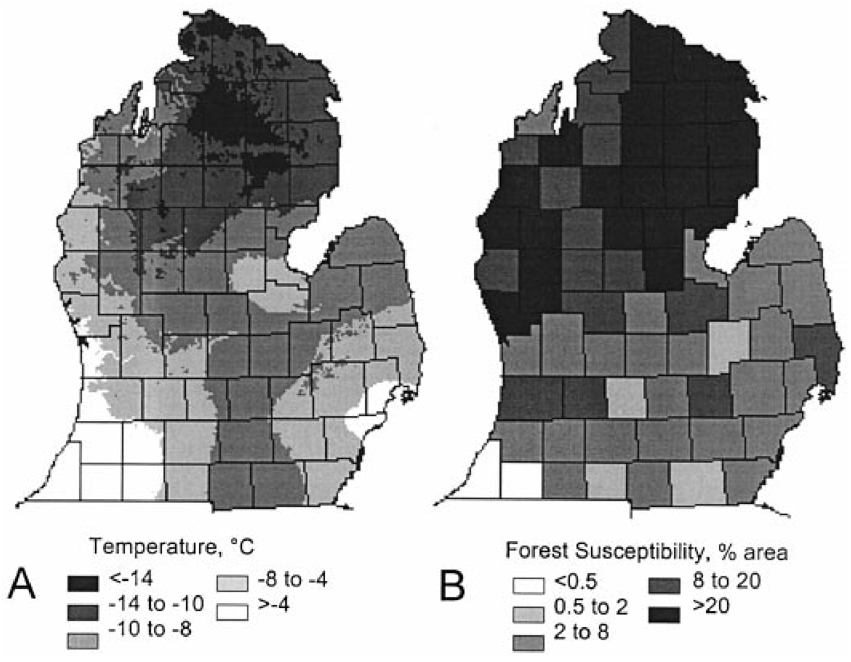

Figure 5 Average minimum January temperature in Michigan in 1986 (A) and forest susceptibility measured as percentage land area that has > 50% tree basal area in preferred species (B).

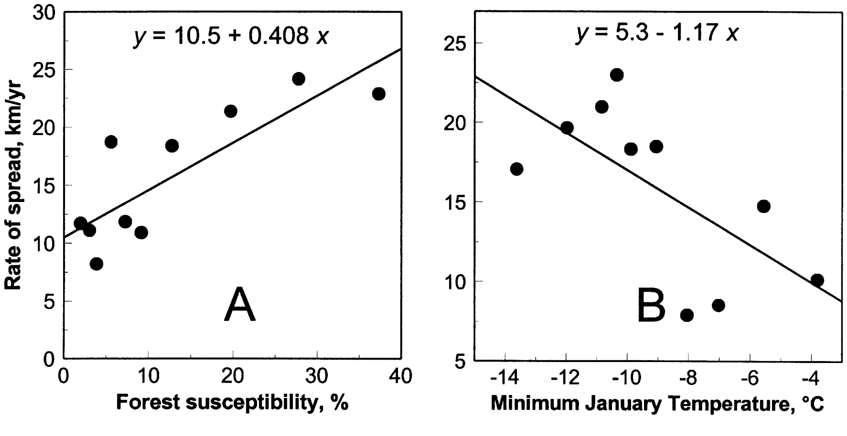

Figure 6 Relationship between the rate of gypsy moth spread in Michigan, forest susceptibility (percentage land area that has > 50% of tree basal area in preferred species) (A), and average minimum January temperature (B). Each point (N = 10) is the average in a group of ≈240 estimates of spread rate. Data were combined for all years and population thresholds and then grouped according to forest susceptibility (A) or temperature (B).

Discussion

This study indicates that the rate of spread in Michigan was not reduced by low winter temperatures. Instead, it was positively correlated with local forest susceptibility. Below we discuss possible explanations of this phenomenon.

The average rate of spread of gypsy moth populations in the lower peninsula of Michigan in 1985–1993 (15.8 km/yr) is similar to rates found in other areas of the U.S.A. Liebhold *et al.* (1992) reported a spread rate of 20.78 km/yr in 1966–1989 in areas with a mean minimum January temperature > -13.8°C. According to Sharov & Liebhold (1997), the rate of spread in the Appalachian Mountains (Virginia and West Virginia) from 1981 to 1990 was 26.5 km/yr, but in 1991–1995 it decreased to 8.6 km/yr, apparently because of intensive pest management in that area.

The rate of spread may depend on numerous ecological processes in the population dynamics of the invading species. The simplest model of population spread was suggested by Skellam (1951). This model combines an exponential population growth with diffusion in space. In this model, the rate of spread depends both on the intrinsic rate of increase, *r*, and diffusion coefficient, *D*, which characterizes dispersal abilities of organisms. Effects of ecological factors on the rate of spread depends on their relationship with these two parameters.

Natural dispersal of gypsy moths is limited. Adult females lay their eggs close to their emergence site because they cannot fly. Newly hatched larvae can disperse on silk threads blown in the wind, but the distance travelled is usually short. More than 99% of dispersing larvae were captured at distances $\leq$ 120 m from the source (Mason & McManus, 1981). Larval dispersal is not sufficient to explain the progression of the population front in North America (Liebhold *et al.*, 1992). There is increasing evidence that inadvertent transportation of gypsy moth egg masses and other life stages by humans is the most important dispersal mechanism that determines the rate of population spread (McFadden & McManus, 1991; Leonard & Sharov, 1995). We do not have data on the transportation of gypsy moth life stages by humans in Michigan, but it is not likely that transportation is correlated strongly with temperature or forest susceptibility, and therefore, is the mechanism by which these factors influence the rate of spread.

Both winter temperature and forest susceptibility may affect the survival rate of the gypsy moth and this would change the intrinsic rate of increase, *r*. Bess (1961) reported that ≈ 90% gypsy moth egg mortality was due to low temperatures in Massachusetts. Williams *et al.* (1990) found no correlation between egg mortality and minimum winter temperature in New Jersey. Winter mortality of gypsy moth eggs is reduced if they are located below snow cover level (Leonard, 1972). In Quebec, the majority of egg masses were located on the trees above 1.5 m, but winter mortality was never higher than 39.7% (Madrid & Stewart, 1981).

In this study, we found a negative correlation between average minimum January temperature and the rate of spread (Fig. 6B), which is difficult to explain by direct effects of temperature because mild winters should be beneficial for egg survival (Bess, 1961; Madrid & Stewart, 1981). This negative relationship apparently resulted from a correlation of temperature with other factors (e.g. forest susceptibility) that may affect population spread. Winters in this area may be sufficiently mild such that they have little effect on egg survival. However, it is possible that in areas with severe winters (e.g. in Canada), low temperatures may substantially affect egg survival and thereby limit the rate of gypsy moth spread. The fact that spread rates were not affected adversely by cold winters does not mean that winter temperatures have no effect on gypsy moth population at all. These effects were recorded in Michigan previously (J. A. Witter, personal communication), but apparently they were not frequent enough to reduce the rate of population spread.

Forest susceptibility is an important factor that affects the performance of gypsy moth populations. Foliage quality determines larval survival, the rate of development, and pupal weight (Barbosa & Capinera, 1977; Hough & Pimental, 1978; Barbosa *et al.*, 1983; Montgomery, 1991; Stoyenoff *et al.*, 1994). Gypsy moth outbreaks are more frequent in areas with a high proportion of susceptible tree species (Liebhold *et al.*, 1994; Witter *et al.*, 1992).

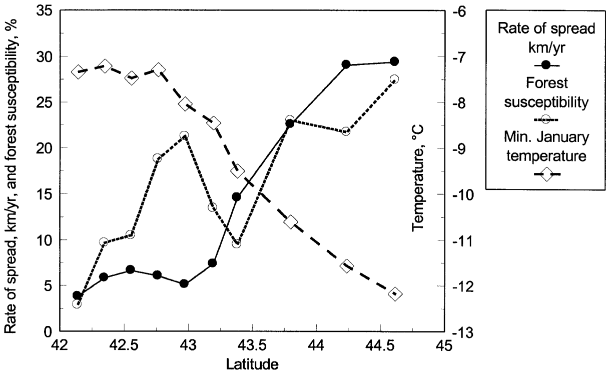

Figure 7 Latitudinal change in the rate of gypsy moth spread in Michigan, forest susceptibility (percentage land area that has > 50% of tree basal area in preferred species) and average minimum January temperature. Each point is the average in a group of ≈240 estimates of spread rate. Data were combined for all years and population thresholds and then grouped according to latitude.

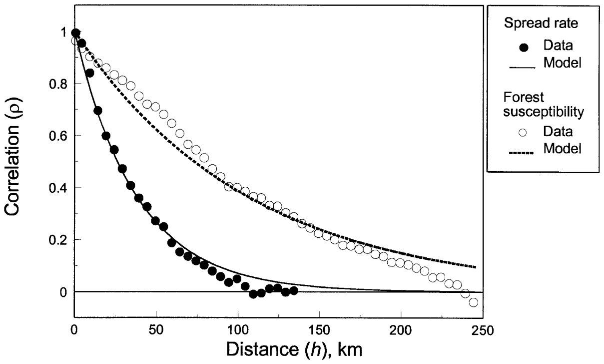

Figure 8 Correlograms of the rate of gypsy moth spread in Michigan and forest susceptibility. The exponential model (eqn 1) was used to fit the data.

There is no universal criterion of forest susceptibility. From a management point of view, susceptibility can be related to the frequency of defoliation (Liebhold *et al.*, 1994). Ecological criteria of susceptibility are fecundity (in the case of gypsy moth, it is correlated to pupal biomass) and mortality (Montgomery, 1991; Stoyenoff *et al.*, 1994). An ethological criterion of susceptibility is foliage preference (Barbosa, 1978). Usually, these criteria are correlated, i.e. high fecundity, low mortality and frequent defoliation are observed on preferred host species. Host susceptibility is even more difficult to define at large spatial scales because additional factors such as spatial autocorrelation of habitat quality may modify the performance of insect populations.

Our measure of forest susceptibility (percentage land area with > 50% basal area in preferred species) characterizes only some aspects of the gypsy moth relationship with host trees. It does not characterize the size of habitat patches, soil types, the presence of tree species with intermediate susceptibility and many other factors. But its advantage is that it is based on existing large-scale forest inventory data. Thus, it was possible to use it for state-wide comparisons of spread rates of gypsy moth populations.

According to Fig. 6(A), the rates of gypsy moth spread in Michigan were ≈ two-fold higher in areas with a high proportion of land area covered by susceptible forests (i.e. > 20%) than in areas with low forest susceptibility (i.e. < 5%). Contiguous susceptible forests are located mostly in the northern half of the lower peninsula (Fig. 5B). The southern half of the lower peninsula is dominated by agriculture and urban land uses, and the proportion of land covered with susceptible stands is smaller. In susceptible areas, the rate of spread was 21–24 km/yr, which is comparable with the rate of spread (26.5 km/yr) observed in the Appalachian mountains of Virginia and West Virginia in 1981–1990 (Sharov & Liebhold, 1997). The Appalachian mountains have contiguous areas with favourable host types, especially along the ridges. The similarity in the rates of population spread in these two areas separated by 500–900 km in a north–south direction gives additional evidence that winter temperatures have little effect on the rate of spread.

This study provides the first quantitative evidence that the spread of gypsy moth populations is affected by forest composition. Further work in this area is needed because that information might be useful in optimizing current efforts to slow the spread of the gypsy moth in North America (Sharov *et al.*, 1998).

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