

# Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity

Kyle J. Haynes · Andrew M. Liebhold ·  
Derek M. Johnson

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**Abstract** Outbreaks of many forest-defoliating insects are synchronous over broad geographic areas and occur with a period of approximately 10 years. Within the range of the gypsy moth in North America, however, there is considerable geographic heterogeneity in strength of periodicity and the frequency of outbreaks. Furthermore, gypsy moth outbreaks exhibit two significant periodicities: a dominant period of 8–10 years and a subdominant period of 4–5 years. In this study, we used a simulation model and spatially referenced time series of outbreak intensity data from the Northeastern United States to show that the bimodal periodicity in the intensity of gypsy moth outbreaks is largely a result of harmonic oscillations in gypsy moth abundance at and above a 4 km<sup>2</sup> scale of resolution. We also used geographically weighted regression models to explore the effects of gypsy moth host-tree abundance on the periodicity of gypsy moths. We found that the strength of 5-year cycles increased relative to the strength of 10-year cycles with increasing host tree abundance. We suggest that this pattern emerges because high host-tree availability enhances the growth rates of gypsy moth populations.

**Keywords** *Lymantria dispar* · Periodicity · Population cycles · Spatial synchrony

## Introduction

Many species of forest-defoliating insects are known to exhibit cyclical population dynamics. Outbreaks in these populations are often periodic (i.e., they occur at statistically regular intervals) and synchronous over broad geographic areas (Berryman 1996; Liebhold and Kamata 2000). Within the range of a single species, however, there may be considerable geographic heterogeneity in the strength of periodicity and the frequency of population cycles (Johnson et al. 2006a; Cooke and Lorenzetti 2006; Volney and McCullough 1994). Moreover, periodicity may differ not only among locations but also across spatial scales. For example, Liebhold et al. (2000) reported that several types of population behavior in forest-defoliating insects such as population cycles, second-order lag correlations, and spatial synchrony, are found only when analyses are conducted over large spatial scales.

Outbreaks of the gypsy moth, *Lymantria dispar* (L.) in North America are significantly periodic when analyzed over broad geographic areas, though the timing of outbreaks is less regular than has been observed in some species of forest-defoliating Lepidoptera (e.g., the larch budmoth, Baltensweiler and Fischlin 1988; Williams and Liebhold 1995). Outbreaks in North American populations of the gypsy moth have been reported to occur approximately every 10 years (Williams and Liebhold 1995; Liebhold et al. 2000; Johnson et al. 2005). It was recently reported, however, that the temporal patterns of gypsy moth outbreaks are more complex. Johnson et al. (2006a) found that gypsy moth abundance fluctuated with a dominant period of 10 years and a subdominant period of 5 years. In addition, the relative strength of 5- and 10-year periodicity varied with forest composition. Five-year periodicity was strongest in forest types where oaks are

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K. J. Haynes (✉) · D. M. Johnson  
Department of Biology, University of Louisiana,  
P.O. Box 42451, Lafayette, LA 70504, USA  
e-mail: kjh1087@louisiana.edu

A. M. Liebhold  
Northern Research Station, USDA Forest Service,  
180 Canfield Street, Morgantown, WV 26505, USA

mixed with pines. The most parsimonious explanation for this bimodal pattern of periodicity in gypsy moth populations is that 5- and 10-year cycles are harmonics, or components, of the overall pattern of population fluctuation. For example, populations in oak-hickory forests had a dominant 10-year cycle but additionally had lower intensity outbreaks on a 5-year cycle. In oak-pine forests, 5-year cycles were dominant and 10-year cycles were subdominant. An alternative explanation is that all populations of gypsy moths underwent approximately 10-year cycles, where some peaked around 1980, 1990, and 2000, while others were in antisynchrony, peaking around 1985 and 1995 (Johnson et al. 2006a). Researchers observed a similar phenomenon in measles epidemics in England; outbreaks in one area fell into the antisynchronous phase with outbreaks in other areas over a period of several years (Grenfell et al. 2001). Outbreaks of the gypsy moth in North America are partially synchronous, but synchrony declines with distance and decays completely over long distances (Peltonen et al. 2002). Outbreaks separated by >600 km were not significantly synchronous (Peltonen et al. 2002). If gypsy moth populations in different locations did fluctuate in antisynchrony, the analysis conducted by Johnson et al. (2006a) could conceivably have artificially introduced the appearance of 5-year cycles. This is because the data they used consisted of a single aggregate time series for each forest type representing the average outbreak intensity over a large portion of the northeastern United States.

Cyclical population dynamics in forest-defoliating insects generally are thought to result from trophic interactions (Turchin et al. 2003; Dwyer et al. 2004), but the factors influencing gypsy moth periodicity remain unresolved. Differences in periodicity among forest stands may be caused by intrinsic differences in forest communities such as differences in the availability of gypsy moth hosts, densities of generalist predators (Campbell and Sloan 1977; Elkinton and Liebhold 1990), or the covariation of these or other factors. For example, oak species dominate as the moth's most preferred hosts in North America (Liebhold et al. 1995) but they also provide the main winter food source (acorns) for generalist predator rodents such as *Peromyscus leucopus*, which prey opportunistically upon gypsy moth pupae (Smith 1985; Yahner and Smith 1991). Given the potential for scale-dependent population behavior and spatial covariation in factors influencing forest insect population growth, advancing our understanding of forest insect outbreaks will require spatially explicit analyses and a multi-scale approach.

In this study, we examined the sources of the 5- and 10-year cycles in the intensity of gypsy moth outbreaks in the northeastern United States. We used a spatially extended simulation model to examine the effects of antisynchrony

and the spatial scale over which spatiotemporal population data are collected on the apparent periodicity of population fluctuations. In addition, we performed wavelet analyses on a 31-year dataset of yearly gypsy moth outbreak intensity. By varying the spatial scale over which the data were aggregated (i.e., the area of sample quadrats), we examined alternative hypotheses (antisynchrony vs harmonic oscillations) about the source of the 5- and 10-year periods of gypsy moth outbreaks. We also examined the effects of gypsy moth host-tree abundance on the relative strength of 5- and 10-year periodicity in the intensity of gypsy moth outbreaks.

## Materials and methods

### Study organism

The gypsy moth, a native of Eurasia and North Africa, feeds on the foliage of over 200 tree species in North America (Liebhold et al. 1995). Trees in the genera *Quercus* (oaks), *Populus* (poplars and aspens), and *Larix* (larch) are the moth's preferred hosts, and outbreaks occur most frequently in forest stands dominated by these trees (Kleiner and Montgomery 1994; Davidson et al. 2001). The gypsy moth usually occurs at such low densities that the species is virtually undetectable, but occasionally densities grow rapidly to outbreak levels resulting in the defoliation of large areas of forest (Liebhold et al. 2000).

### Antisynchrony model

We explored the extent to which spatial aggregation of synchronous and antisynchronous outbreak intensity data from multiple locations affected the relative strength of 5- and 10-year periods using a spatially extended stochastic second order log-linear model (Royama 1992):

$$X_{i,t} = \beta_0 + (1 + \beta_1)X_{i,t-1} + \beta_2X_{i,t-2} + e_i.$$

The variable  $X_{i,t} = \log(N_{i,t})$ , where  $N_{i,t}$  is the abundance at location  $i$  in generation  $t$ . The first term,  $\beta_0$ , which has no effects on the dynamical properties of the model, was set to zero. The parameters  $\beta_1$  and  $\beta_2$  represent the strength of density dependence at time lags of 1 and 2 years, respectively. To mimic the magnitude and 10-year period of fluctuations in gypsy moth abundance, we set  $\beta_1$  and  $\beta_2$  at 0.48 and  $-0.87$ , respectively. The fourth term,  $e_i$  is zero-mean, normally distributed environmental stochasticity in population growth. Based on a general understanding that such stochasticity arises from a combination of local ( $s$ ) and regional ( $r$ ) processes, we modeled  $e_i$  as the mixture  $r\rho_{i,t} + (1 - r)\sigma_t$ , where  $\rho_{i,t}$  and  $\sigma_t$  represent zero-mean random Gaussian variates each with a variance  $u$ , and  $r$

represents the relative importance of the local versus regional variability (Johnson et al. 2006b). We arbitrarily set  $u$  at 0.25. Based on empirical estimates, we set the regional versus local stochasticity at 75% and 25%, respectively (Peltonen et al. 2002).

An initial population size for each of 1,000 locations was assigned by randomly drawing from a normal distribution with a mean of 20 and standard deviation of 1. We ran the model for 500 time steps (years). From the time series resulting from a single run of the model, we generated two datasets: an unmanipulated set without antisynchrony and another set with antisynchrony. We introduced antisynchrony among locations by randomly choosing half of the 1,000 populations and shifting the time series of these populations 5 years (half the duration of a population cycle) into the future. For each dataset, we then aggregated data across multiple locations. The time series were either not aggregated, or aggregated into groups of 5, 10, or 50. A single time series was produced for each group by computing the average population abundance at each time step. For each level of data aggregation, we examined the periodicity of the time series using wavelet analysis (Torrence and Compo 1998). Wavelet analysis is a method for extracting frequency information from a signal, and can be applied to time series where the frequency and amplitude of oscillations in the signal change through time (Torrence and Compo 1998). Computation of the continuous wavelet transform involves sliding wavelets (zero-mean mathematical functions exhibiting oscillations that are localized in time; Farge 1992; Torrence and Compo 1998) of varying temporal scale (width) across a time series to measure how well wavelets of different scale approximate the actual data (Torrence and Compo 1998). The frequency of oscillations in the real data can then be readily estimated based on the relationship between the scale and the period of the wavelet function. We quantified population fluctuations using the Morlet wavelet, an exponential function exhibiting damped, periodic oscillations (Farge 1992; Grenfell et al. 2001). To reduce the influence of transient dynamics resulting from initial conditions, the first 50 years of data from each simulated time series were discarded prior to conducting the wavelet analysis.

#### Historical outbreak data

Periodicity in gypsy moth outbreaks were assessed by analyzing annual aerial defoliation survey maps from the northeastern United States over a period of 31 years (1975–2005). This time series is a superset of the 28-year (1975–2002) series analyzed by Johnson et al. (2006a). These maps were digitized and represented as sequential raster layers in a geographic information system (GIS). Analyses here were restricted to regions designated as part of the

1975 generally infested area in USDA gypsy moth quarantine regulations. Data from areas more recently infested by the gypsy moth were not included in our analysis because their invasion history precluded defoliation in earlier years, thus affecting long-term temporal patterns. We also excluded any quadrats in which <3 defoliation events were detected. Additional details of the aerial survey methods used to quantify defoliation levels are found in Liebhold et al. (1997) and Johnson et al. (2006a).

To evaluate whether 5-year cycles in gypsy moth abundance are real or are artifacts of antisynchrony between populations in different locations, we examined how the spatial scale of aggregation affected our ability to detect 5-year periodicity in the gypsy moth defoliation time series. Defoliation time series were compiled for square quadrats ranging in size from 4 to 4,096 km<sup>2</sup> (4, 16, 64, 256, 1,024, and 4,096 km<sup>2</sup>). Periodicity in each of the time series data was examined with wavelet analysis using the Morlet wavelet function (Torrence and Compo 1998). We examined how the relative strength of 5- to 10-year periodicity changed with quadrat area. The relative strength of these two periodicities was calculated as the ratio of the strength of 5-year (4–6 years) periodicity to the strength of 10-year (8–12 years) periodicity. For each periodogram, the maximum powers observed between 4–6 year and 8–12 year periods were used as measures of the strengths of 5 and 10-year periodicity, respectively. Because Johnson et al. (2006a) found that periodicity within a quadrat was affected by the dominant forest type group, the ratio of periodicities was computed separately for quadrats dominated by each of four different forest type groups: oak-hickory, oak-pine, maple-beech-birch, and white-red-jack pine. These forest type groups were designated in a map that classified forest stands across the United States based on tree species composition (Eyre 1980). We used a GIS to determine the dominant forest type group in the Eyre (1980) map layer for each quadrat.

The relationships between gypsy moth host tree abundance and the strength of 5- vs 10-year periodicity of gypsy moth outbreaks were determined by wavelet analysis of the defoliation time series from each of 60,182 4 km<sup>2</sup> quadrats. Host tree abundance was based upon a 1 km raster GIS layer developed by Morin et al. (2004). Host abundance was measured as the basal area per hectare of host tree species that are preferred hosts (Liebhold et al. 1995). This raster GIS layer was developed by interpolating host basal area from >90,000 forest inventory plots (Kingsley 1985) and then adjusting for forest density by multiplying interpolated host basal area by percentage forest cover (Morin et al. 2004). Seventy-nine tree species in eastern North America are considered to be preferred hosts, but oaks (*Quercus* spp.) are the dominant component of preferred hosts in the Northeastern United States (Liebhold et al.

1995). The strengths of 5- and 10-year periodicity within each of the quadrats were measured as the maximum power from the periodicity spectra for periods of 4–6 and 8–12 years, respectively.

We evaluated the effects of host abundance on the ratio of the strength of 5- to 10-year periodicity with ordinary least-squares regression (OLSR) and geographically weighted regression (GWR). OLSR and GWR provide complementary information when examining relationships between environmental variables and dependent variables of interest using data collected at multiple locations. OLSR is useful for providing a single, global parameter estimate for each environmental variable, but OLSR models cannot account for spatial autocorrelation or nonstationarity (defined as spatial heterogeneity in the relationships between environmental variables and dependent variables across space; Fotheringham et al. 2002). GWR models do not provide a global estimate of each parameter, but they explicitly incorporate spatial dependence and nonstationarity. In GWR, a local regression model is generated for each sampled location by using data from the focal location as well as data from nearby locations. The data are weighted such that weights ( $w_i$ ) decrease with increasing distance from the focal location. We used an exponential weight function given by

$$w_i = \sqrt{\exp\left(\frac{-d_{ij}}{\theta}\right)}$$

where  $d_{ij}$  is the distance between the focal location  $i$  and data point  $j$  (Brundson et al. 1996). The scalar decay parameter,  $\theta$ , was determined using cross validation, a procedure in which the optimal value of  $\theta$  is the value that minimizes the score function

$$\sum_{i=1}^n (y_i - \hat{y}_{\neq i})^2$$

where  $\hat{y}_{\neq i}$  represents the predicted value for  $y_i$  with the data from location  $i$  omitted from the calculation (Fotheringham et al. 2002). We tested for nonstationarity of the host abundance regression parameter using a Monte Carlo method described in Brundson et al. (1996). The geographic coordinates of the quadrats were randomly permuted against the other variables 100 times, each time performing GWR and calculating the variance of the local parameter estimates. We then compared the variance estimated from the GWR using the real data to the experimental distribution of variances to obtain the significance level.

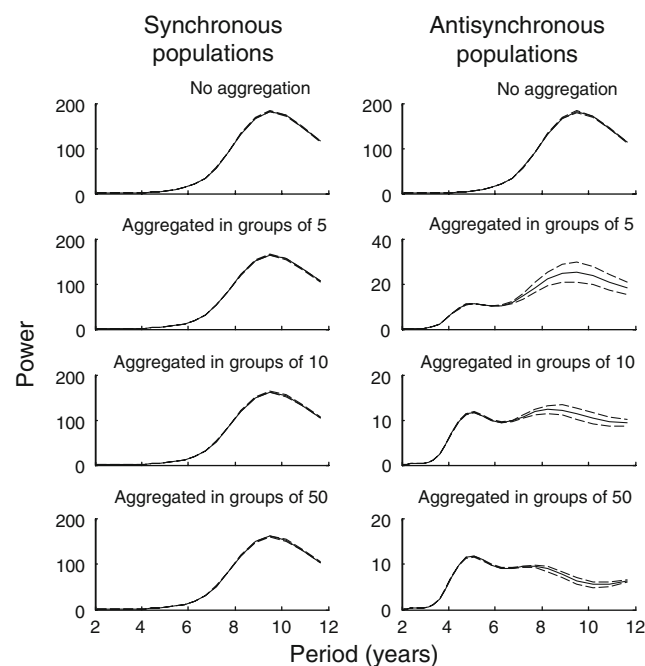
Prior to analyses above, the ratio of the strength of 5- to 10-year periodicity was  $\ln$  transformed to minimize heterogeneity of variance. All analyses were carried out using the Matlab programming language. The GWR models were

estimated using James LeSage's econometrics toolbox for Matlab, which can be downloaded from <http://www.spatial-econometrics.com/>.

## Results

### Antisynchrony model

The regional stochasticity included in the autoregressive population models resulted in highly synchronized fluctuations in the 1,000 simulated populations. Wavelet analysis of the time series of these synchronized populations revealed wavelet power spectra with a dominant period of approximately 10 years (Fig. 1). Furthermore, no populations in the unmanipulated datasets with synchronous populations exhibited a dominant period of 5 (4–6) years (Table 1). When antisynchrony was introduced by shifting half of the 1,000 populations 5 years into the future, the effect of aggregating data was quite different. The strength of 5-year periodicity increased relative to the strength of 10-year periodicity with increasing levels of data aggregation (Fig. 1). When the time series were aggregated into groups of 5 or 10, the periodograms became decidedly bimodal with peaks in the strength of periodicity near 5 and 8–9 years. At the highest level of aggregation (50 time series per group), the periodogram indicated a dominant 5-year periodicity (Fig. 1).



**Fig. 1** Wavelet analysis of the simulated time series ( $\log_{10}$ -transformed gypsy moth population size) for 1,000 locations with and without introducing antisynchrony among locations. *Solid lines* Mean strength of periodicity, *dashed lines* 95% confidence intervals

**Table 1** The effect of aggregating gypsy moth outbreak intensity time series data over multiple locations in the presence and absence of antisynchrony among locations

Level of aggregation	Proportion of time series with a dominant period of 4–6 years	
	No antisynchrony	Antisynchrony
No aggregation	0	0
Groups of 5	0	0.29
Groups of 10	0	0.59
Groups of 50	0	0.95

Historical outbreak data

Wavelet analysis of gypsy moth defoliation time series revealed that, on average, the strength of periodicity peaked similarly near 5 and 10 years regardless of quadrat size (Fig. 2). In addition, the dominance of 5-year periodicity was largely unrelated to the size of sample quadrats; for each habitat type, the 95% confidence intervals around the ratio of the strength of 5-year periodicity to the strength of 10-year periodicity broadly overlapped across the different quadrat sizes (Fig. 3).

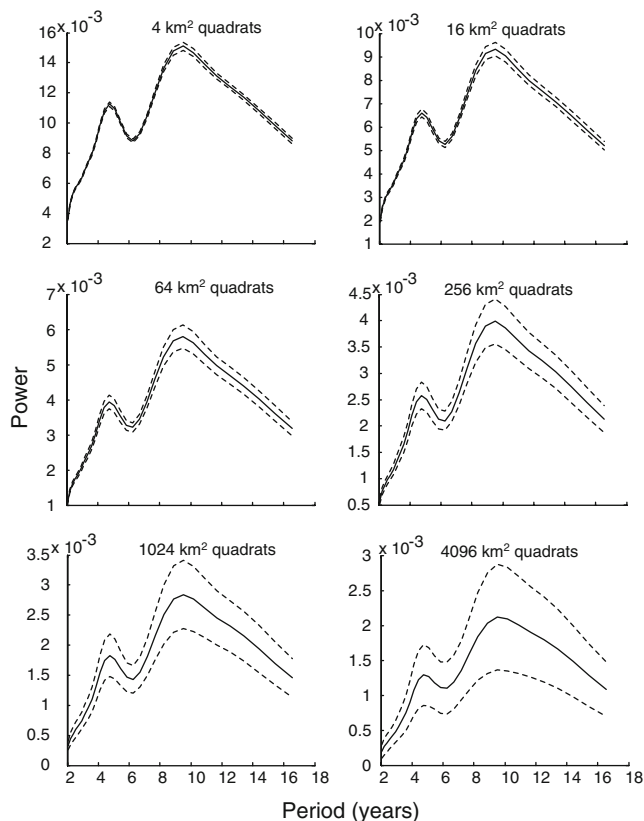
There was considerable geographic overlap between areas where the gypsy moth exhibited strong 5- and 10-year

periodicity (Fig. 4), evidenced by a weak positive correlation between the strength of 5-year periodicity and the strength of 10-year periodicity ( $n = 7084$ ,  $r = 0.088$ ,  $P < 0.001$ ). The strength of both 5-year periodicity ( $r = 0.458$ ,  $P < 0.001$ ) and 10-year periodicity ( $r = 0.361$ ,  $P < 0.001$ ) increased significantly with the frequency of years in which defoliation was observed within a quadrat. However, there was significant geographic variation in the relative strength of 5- versus 10-year periodicity, measured as the ratio of the strengths of these two periods (5-year/10-year). Based on non-spatial OLSR, the ratio increased significantly with the basal area of preferred host trees (Table 2), and the ratio was uncorrelated with defoliation frequency ( $r = 0.015$ ,  $P = 0.221$ ). However, this model explained only 2.2% of the geographic variation in the relative strength of 5- versus 10-year periodicity (based on the  $r^2$  value).

In contrast, the aggregate GWR model explained 71.3% of the variation in the relative strength of 5- to 10-year periodicity. On average, the local regressions indicated a positive relationship between host basal area and the ratio of the strength of 5-year periodicity to 10-year periodicity (Table 3). The effect of host basal area was significant in 64% of the local regressions ( $\alpha = 0.05$ ). Cross validation procedures selected an exponential decay parameter of 4.47, which results in a steep decline in the weight given to data with increasing distance. For example, the weight given to data decayed to 0.1 when the distance from a focal quadrat reached 8.94 km. Finally, we found significant nonstationarity in the effect of host basal area ( $P < 0.01$ ) on the relative strength of 5- to 10-year periodicity, based on a Monte Carlo simulation, which revealed greater differences in the regression coefficient among locations than expected by chance.

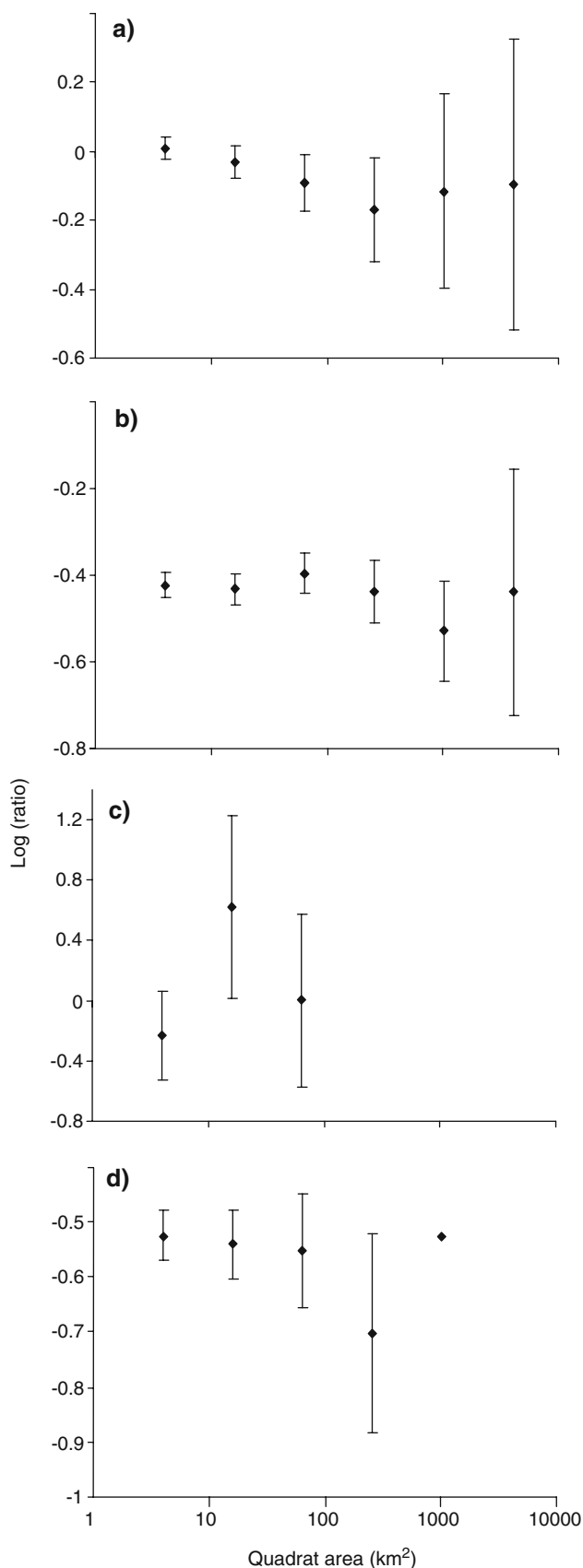
Discussion

Our results appear to rule out the possibility that antisynchronous dynamics are responsible for bimodality in the periodicity of gypsy moths at scales of 4 km<sup>2</sup> and larger. For simulated populations that fluctuated with a 10-year periodicity but in antisynchrony with one another, the shape of the periodogram was strongly influenced by the spatial scale over which time-series data were aggregated; the periodogram was unimodal if the data were not aggregated, but was strongly bimodal if the data were aggregated over large areas (Fig. 1). The spatial scale over which the historical gypsy moth outbreak data were aggregated, however, had no such effects. We found strongly bimodal periodicity in gypsy moth density regardless of quadrat size (Fig. 2). Moreover, by inspecting the spatial variation in the strength of 5- and 10-year



**Fig. 2** Wavelet analysis of the  $\log_{10}(x + 1)$  transformed gypsy moth yearly outbreak probability data for each quadrat size. Solid lines Mean strength of periodicity, dashed lines 95% confidence intervals





◀ **Fig. 3a–d** Effects of aggregation of sampling quadrats on the ratio of the strengths of 5- and 10-year periodicity (5-year/10-year) in time series of levels of gypsy moth defoliation in quadrats dominated by one of four forest type groups (means  $\pm$  95% CI). **a** Oak-hickory, **b** maple-beech-birch, **c** oak-pine, **d** white-red-jack pine

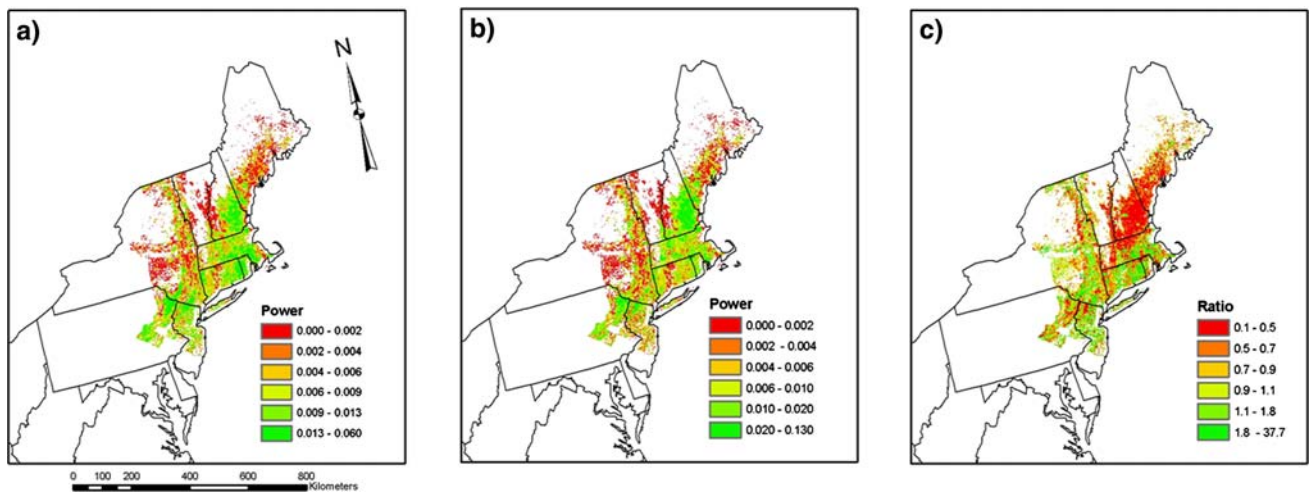
**Table 2** Results from ordinary least-squares regression (OLSR) model showing the relationship between host tree abundance and log (strength of 5-year defoliation periodicity/strength of 10-year defoliation periodicity)

Source	Coefficient	SE of coefficient	<i>t</i>	<i>P</i>
Constant	−0.437	0.010	−19.761	<0.001
Preferred hosts (%)	0.054	0.004	12.560	<0.001

periodicity, we have found that there was broad overlap among quadrats with strong 5-year periodicity and quadrats with strong 10-year periodicity (Fig. 4). Thus, it appears that 5-year cycles and 10-year cycles were harmonics, i.e., component cycles superimposed on one another. Harmonic population fluctuations have also been found in a mechanistic model of gypsy moth–predator–pathogen interactions (O.N. Bjørnstad et al., unpublished data). In this model, harmonic fluctuations appeared only when the carrying capacity of the predator (a generalist predator exhibiting a type-II functional response) was high. To date, few studies have reported harmonic oscillations in population size by forest insects or animals of any kind (but see Cooke and Lorenzetti 2006; Klvana et al. 2004).

In spite of the geographic overlap between areas where gypsy moth outbreaks occurred at 5- and 10-year cycles, we found substantial geographic variation in the relative strength of 5- and 10-year periodicity in gypsy moth outbreaks. One potential explanation for why the strength of 5-year periodicity increased with increasing abundance of preferred host tree species is that gypsy moth population growth rates may be higher in areas dominated by preferred-host trees. Reduced survivorship and fecundity of gypsy moths feeding on less-preferred tree species (Hamilton and Lechowicz 1991), for example, might result in low population growth rates in forest stands with low densities of preferred hosts. In forest defoliating Lepidoptera, higher rates of population growth or immigration may shorten the time required for populations to recover from a population crash and also hasten population crashes (Johnson et al. 2006c), which are caused by density-dependent mortality (Elkinton and Liebhold 1990; Dwyer et al. 2004).

Though there is substantial geographic variation in periodicity, the gypsy moth only exhibits dominant periods of discrete values, i.e., ca. 5 or ca. 10 years; we do not see the dominant period varying along a continuum of intervals between 5 and 10 years. The constraint of gypsy moth oscillations to either 5- or 10-year periods may be attributed



**Fig. 4a–c** Spatial variation in the strength of periodicity in gypsy moth defoliation. **a** Strength of 5-year periodicity, **b** strength of 10-year periodicity, **c** ratio of the strength of 5- and 10-year periodicity (5-year/10-year)

**Table 3** Results of 7,084 local regressions of the effects of host tree abundance on log (strength of 5-year defoliation periodicity/strength of 10-year defoliation periodicity)

Source	Mean coefficient	SE of mean coefficients	Proportion of regressions in which effect was significant
Constant	−0.248	0.017	0.674
Preferred trees (%)	0.018	0.005	0.643

to multitrophic interactions. When gypsy moth densities are low, population growth is thought to be influenced mainly by generalist rodent predators (predominantly *Peromyscus leucopus*, Elkinton and Liebhold 1990; Elkinton et al. 1996). In the eastern United States, *Peromyscus* populations exhibit large fluctuations in density, with population crashes occurring approximately every 4–6 years (Wolff 1996; Elias et al. 2004). These regular crashes of *Peromyscus* populations have been attributed, in part, to periodic fluctuations in the abundance of red oak acorns, an important mast crop for these mice. The 4–6 year cycle of crashes of *Peromyscus* populations might create a “window” during which gypsy moth populations synchronously release to outbreak levels. In stands where small mammal predators are not abundant, gypsy moth populations may release to outbreak levels every “window”, but in stands with an abundance of small mammal predators, gypsy moth populations may recover from a crash more slowly, thus allowing for a release only every other “window”. Consistent with this hypothesis, Johnson et al. (2006a) reported that gypsy moths had a dominant 5-year period and no indication of a 10-year period in areas where oaks grow in dry soils (e.g., oak-pine forests), which tend to support low densities of generalist rodent predators (Smith 1985; Yahner and Smith 1991; Liebhold et al. 1995).

Furthermore, a given population may display both 5- and 10-year period (i.e., harmonic oscillations) because temporal variation in predator densities or demographic or environmental stochasticity may sometimes result in outbreaks occurring during consecutive “windows” and other times only every other “window”.

Our findings also reveal substantial spatial heterogeneity in the effect of host tree abundance on the relative strength of 5- versus 10-year cycles in gypsy moth outbreaks. Numerous studies have documented geographic variation in periodicity of animal populations (e.g., Bjørnstad et al. 1995, 1996; Fromentin et al. 1997). Yet, we are aware of no other studies that have considered the possibility of spatial heterogeneity in relationships between environmental factors and the periodicity of population fluctuations. The spatial heterogeneity in the effect of host abundance on gypsy moth periodicity would not have been detected with statistical approaches that assume that the effects of environmental variables are constant across space (e.g., OLSR or spatial autoregression models, Fotheringham et al. 2002). Possible sources of nonstationarity include covariation of measured environmental variables with unmeasured variables or interactive effects (Fotheringham et al. 2002). In this system, for example, the direction or strength of the relationship between host abundance and the strength of 5-year periodicity could conceivably be dependent on an additional environmental factor that also affects gypsy moth population dynamics.

This study describes a novel approach for distinguishing between two alternative sources of bimodal periodicity—antisynchrony between spatially disjunct populations or harmonic population oscillations—as proposed in Johnson et al. (2006a). For the gypsy moth, our findings support the hypothesis of harmonic population oscillations and rule out

the possibility of extensive antisynchrony at scales of 4 km<sup>2</sup> and larger. Finally, whereas harmonic oscillations in the gypsy moth likely originate due to local processes such as tritrophic interactions involving rodent predators and gypsy moth pathogens (O.N. Bjørnstad et al., unpublished data), our study shows that geographic variation in the degree to which gypsy moth populations exhibit harmonic oscillations (i.e., where a 5-year cycle is superimposed on the dominant 10-year cycle) is influenced by the availability of preferred hosts.

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