

Geographical variation in the periodicity of gypsy moth outbreaks

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The existence of periodic oscillations in populations of forest Lepidoptera is well known. While information exists on how the periods of oscillations vary among different species, there is little prior evidence of variation in periodicity within the range of a single Lepidopteran species. The exotic gypsy moth is an introduced foliage-feeding insect in North America. Its populations are characterized by high amplitude oscillations between innocuously low densities and outbreak levels during which large regions of forests are defoliated. These outbreaks are recognized to arise periodically with considerable synchrony across much of the gypsy moth's North American range. Our analysis indicates that gypsy moth outbreaks in North America are periodic but they exhibit two dominant periodicities: a primary period of 8–10 yr (as previously reported) and a secondary period of 4–5 yr (a new finding in this study). The outbreak periodicity varied geographically and this variation was associated with forest type. We found that in the most susceptible forest types, those on xeric sites where oak is often mixed with pines, outbreak periodicity had a more dominant 5-yr period while in forest types characteristic of more mesic sites where oak was mixed with maples and other species, cycles were clearly operating on a 10-yr period.

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Several species of forest Lepidoptera are known to exhibit extreme fluctuations in abundance, varying from very low (almost undetectable) densities, but occasionally growing to outbreak levels during which they defoliate large tracts of forest. These Lepidopteran outbreaks are commonly periodic (defined as the occurrence of outbreaks over statistically regular intervals), and often occur at approximately 10-yr cycles (Berryman 1996, Liebhold and Kamata 2000). With most of these forest insects, there is a large body of literature on how geographical variation in forest composition affects the periodicity and/or the probability of outbreaks (Maclean and MacKinnon 1977, Anderson and May 1980, Alfaro et al. 1999, Davidson et al. 2001). Note that probability differs from periodi-

city in that some parcels of forest may never exhibit outbreaks (outbreak probability of zero) but outbreak periodicity could not be defined for these areas. There is almost nothing known about how geographical variation in forest composition affects periodicity. Because periodicity is generally thought to result from trophic interactions (Bulmer 1974, Gilg et al. 2003, Turchin et al. 2003, and Dwyer et al. 2004), one may expect that geographical variation in forest communities could lead to geographical variation in periodicity.

Like many other forest Lepidoptera, populations of the gypsy moth *Lymantria dispar* in North America are known to exhibit extreme fluctuations in population density (Montgomery and Wallner 1988). These outbreaks are somewhat periodic and synchronous when

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analyzed across large spatial scales over the northeastern United States (Williams and Liebhold 1995, Peltonen et al. 2002). At smaller spatial scales (e.g. among 1 km² quadrats), however, outbreaks are spatially heterogeneous and are frequently out of synch among locations (Appendix Movie S1).

Gypsy moth larvae feed on the foliage of over 200 tree species in North America (Liebhold et al. 1995b). Several studies have quantified variation among different forest types in their susceptibilities to the gypsy moth as measured by the probability of outbreaks (Kleiner and Montgomery 1994, Davidson et al. 2001). A common finding of these studies is that forest susceptibility is closely related to the proportion of stand composition that is represented by tree species that are highly preferred by gypsy moth larvae. Consequently, gypsy moth outbreaks worldwide most commonly occur in forest stands dominated by host trees in the genera *Quercus* (oak), *Larix* (larch), and *Populus* (poplars and aspens) (Bess et al. 1947, Houston and Valentine 1977, Gottschalk 1993). While populations may persist in stands with lower densities of preferred species, outbreaks appear to be much less probable.

In this study, we use the gypsy moth in the northeastern United States as a model system to study how outbreak periodicity varies geographically and is related to forest type. We demonstrate that, in contrast to previous studies of geographical variation in periodicity of rodent populations for instance, periodicity in the gypsy moth is not a continuous smooth transition (Bjørnstad et al. 1995, 1996), but instead is bimodal with populations either exhibiting periodicity of ca 10 yr and/or 5 yr. Detailed analysis of the outbreak data shows that the 5-yr periodicity was stronger in the more xeric forest types, while 10-yr periodicity was more dominant in mesic forests.

Methods

In this study, we use gypsy moth defoliation data as a proxy for abundance. There are many previous studies that document the statistical association between gypsy moth density (measured numbers of egg masses per ha) and defoliation both through time (Gansner et al. 1985, Williams et al. 1991, Liebhold et al. 1993) and space (Gribko et al. 1995, Liebhold et al. 1995a, 1998). The gypsy moth defoliation data used in this study were derived from sketch maps made during annual aerial surveys conducted in each state in the northeastern United States during the seasonal period of maximum defoliation by the gypsy moth. Canopy defoliation is considered to be detectable at levels >30% during aerial surveys (Webb et al. 1961). We compiled aerial survey data from 1975 to 2002 using methods described in Liebhold et al. (1997). Briefly, defoliation maps from

1975–1995 were not available in digital format so we scanned paper defoliation maps from each state, georeferenced resultant raster files and compiled all state maps to form a single mosaic map for each year. Resultant raster geographical information system (GIS) files were composed of 1 × 1 km cells according to a Lambert azimuthal equal-area projection (Snyder 1987). Defoliation data from 1996 to 2002 were obtained as digitized polygonal files and were converted to 1 km raster GIS files using a vector to raster GIS conversion. During the period studied (1975–2002), the gypsy moth was expanding its range in the northeastern United States. Because some areas only became infested during the latter portion of this period, the lack of defoliation during the early portion of the period in these locations was due to the pattern of invasion and therefore could not exhibit population oscillations. Therefore, we omitted data from regions that were not part of the “area generally infested by the gypsy moth” (as defined in yearly USDA gypsy moth quarantine regulations) prior to 1975. In addition, the gypsy moth’s entire range in Michigan was excluded because it was a disjunct population that was not included in the “infested area” until 1981. We also excluded all quadrats in which defoliation was never detected – see Peltonen et al. (2002) (Fig. 1d) for a map of the area used in this analysis. We plotted time series of the defoliation by the gypsy moth both spatially-averaged across the entire study area, and for aggregated data from each of five forest type groups.

We performed wavelet analysis on the time series of area defoliated across the entire study area ($\log_{10}[x+1]$ transformed, detrended, and normalized to $\bar{x}=0$ and $SD=1$) to quantify outbreak cycle strengths across a range of periodicities (2–16 yr). Wavelet analysis is a time series analysis for identifying periodicity in time series data (Torrence and Compo 1998). Wavelet analysis is similar to Fourier analysis in that the total variance in the time series is partitioned among components at different periodicities (so-called scales). An advantage of wavelet analysis over Fourier analysis, for example, is that it can detect temporal variation in periodicity across

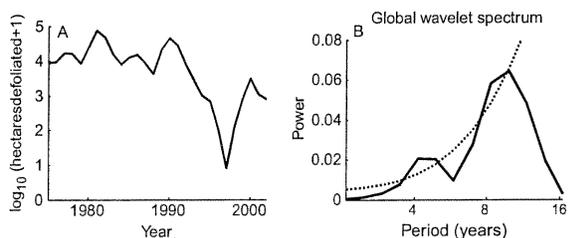


Fig. 1. Wavelet time series analysis for the $\log_{10}(x+1)$ transformed gypsy moth yearly outbreak intensity data over the entire northeastern United States data analyzed here. A) The time series. B) Temporally-global strength of periodicities (thick lines). Values above the thin (monotonically increasing) line indicates significant periodicities.

a time series. The Morlet wavelet function (a damped complex exponential) was used to describe periodicities in the data (Grenfell et al. 2001). We also performed separate wavelet analyses on the outbreak probability aggregated from quadrats dominated by each of five forest type groups (white-red-jack pine, loblolly-shortleaf pine, oak-pine, oak-hickory, and maple-beech-birch) to identify forest type-specific periodicities in gypsy moth outbreaks. These forest type groups represent a generalized system for classifying forest composition and each group encompasses more specific forest types (e.g. oak-hickory includes hawthorn, bear oak, chestnut oak, etc. forest types) (Eyre 1980, Hansen et al. 1992) (online at <http://ncrs.fs.fed.us/pubs/gtr/gtr_nc151.pdf>). Despite the generic nature of this classification system, it is particularly valuable when analyzing large-scale processes as in this study. The geographical extent of each forest type group was extracted from a 1:7 500 000 map of the conterminous USA compiled by the USDA Forest Service Forest Inventory and Analysis (FIA) project in 1967 (Kingsley 1985) and published by the Society of American Foresters (SAF) (Eyre 1980) (Appendix Fig. S1).

We tested for significant differences in periodicity among forest types using logistic regression analysis. Each 1 km² quadrat of forest was categorized as either having a dominant 5-yr or 10-yr periodicity (dummy variables set a 0 and 1, respectively). In the logistic equation,

$$p_i = \frac{\exp(a_i + b_1 f_{1,i} + b_2 f_{2,i} + b_3 f_{3,i} + b_4 f_{4,i} + b_5 f_{5,i})}{1 + \exp(a_i + b_1 f_{1,i} + b_2 f_{2,i} + b_3 f_{3,i} + b_4 f_{4,i} + b_5 f_{5,i})}$$

the probability that the dominant periodicity of quadrat *i* is 10 yr is indicated by the value *p_i*. To account for spatial correlation, the data were divided into 30 by 30 km quadrats, and we calculated the local probabilities (independent of forest type) of 5 vs 10 yr dominant periodicities for each quadrat. These local probabilities were inserted into the logistic equation as the value *a*. Five dummy variables were created to reflect forest type of each 1 km² quadrat (*f*₁ = 1 for white-red-jack pine, otherwise *f*₁ = 0, *f*₂ indicates loblolly-shortleaf pine, *f*₃ indicates oak-pine, *f*₄ indicates oak-hickory, and *f*₅ indicates maple-beech-birch). An iterative improvement method was used to estimate the maximum likelihood effects of forest type on outbreak periodicity (indicated by the parameters *b_j* where *j* corresponds to forest types as indicated in the parameters *f_j*). Akaike's Information Criterion (AIC) (Akaike 1973) was used to determine whether forest type had a significant effect on outbreak periodicity by comparing the likelihood with forest type effects to that with no forest type effects (all *b*'s = 0). Because there were five forest types in the analysis, AIC was penalized to account for four free parameters.

We calculated the mean and 95% confidence interval of the probability of an outbreak for each forest type group over all 1 km² rasters (including those with no outbreaks) per year. The 95% confidence interval was calculated by bootstrapping the data with replacement 1 000 times and reporting the respective boundaries of the 95th percentile. The bootstrap method was used to estimate the 95% confidence intervals rather than using classic statistical techniques because it makes no a priori assumptions regarding the distribution of the data.

Results

The time series of total (over the entire spatial extent) defoliation area indicates sharp peaks in gypsy moth outbreaks around 1980, 1990, and 2000, and minor outbreaks around 1976 and 1986 (Fig. 1A). There was a dominant periodicity of around 8–10 yr and a sub-dominant periodicity around 4–5 yr (Fig. 1B). Both of these periodicities were significant (the critical levels are indicated on Fig. 1B by values above the significance line).

Visual inspection of the defoliation time series reveals intriguingly different temporal patterns of defoliation among the five forest type groups (Fig. 2). While all forest type groups displayed peaks in defoliation around the years 1980 and 1990, the oak-pine and loblolly-shortleaf pine groups tended to have high levels

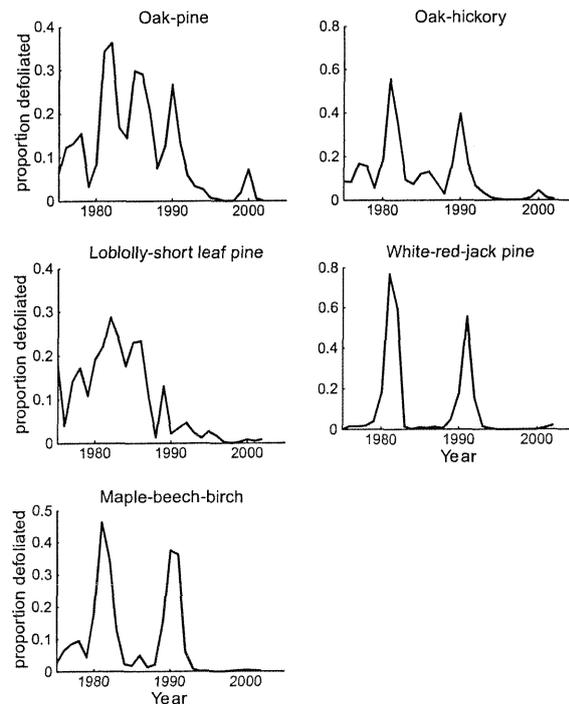


Fig. 2. Time series of defoliation probability by the gypsy moth in five forest type groups in northeastern north America.

of defoliation in some “off-peak” years as well. Alternatively, off-peak defoliation in the oak–hickory forest type group was moderate, while it was low to nearly undetectable in white–red–jack pine and maple–beech–birch forest type groups. Gypsy moth outbreak probability was greatest in forest type groups in which oaks represent a major component (oak–pine, oak–hickory, and loblolly–shortleaf pine forests), those forest type groups with high to moderate off-peak defoliation, while those forest type groups with a smaller component of oak had fewer outbreaks (Table 1) (note that the number of outbreaks in Table 1 is not an indicator of periodicity because many quadrats in this analysis had no outbreaks over the 28-yr period).

Wavelet power spectra illustrate interesting similarities and differences in periodicities of gypsy moth outbreaks across forest type groups (Fig. 3). Populations in the oak–pine forest type group had a strong and significant periodicity at 4–5 yr. Those in oak–hickory also had a strong and significant periodicity at 4–5 yr, and had a strong but insignificant periodicity at 8–10 yr. Populations in loblolly–shortleaf pine, white–red–jack pine, and maple–beech–birch all had dominant periodicities at 8–12 yr (significant in white–red–jack pine and maple–beech–birch forests) with minor subdominant periodicities around 4–5 yr (also significant in white–red–jack pine and maple–beech–birch forests). Thus, in general, populations in oak–pine and oak–hickory forest type groups had strong significant periodicities of 4–5 yr and those in white–red–jack pine and maple–beech–birch had strong significant periodicities at 8–12 yr and lesser, but significant, periodicities at 4–5 yr. Loblolly–shortleaf pine populations had no significant periodicity. Spatial logistic regression analysis revealed that these differences in periodicity among forest types was significant (AIC = 11.52, DF = 4, $n = 79,876$, $p < 0.05$). The forest type effect parameters were $b_1 = 0.01$ (white–red–jack pine), $b_2 = 0.08$ (loblolly–shortleaf pine), $b_3 = -0.20$ (oak–pine), $b_4 = 0.01$ (oak–hickory), and $b_5 = 0.01$ (maple–beech–birch), indicating that the forest type effect was driven by a strong difference between loblolly–shortleaf pine, which

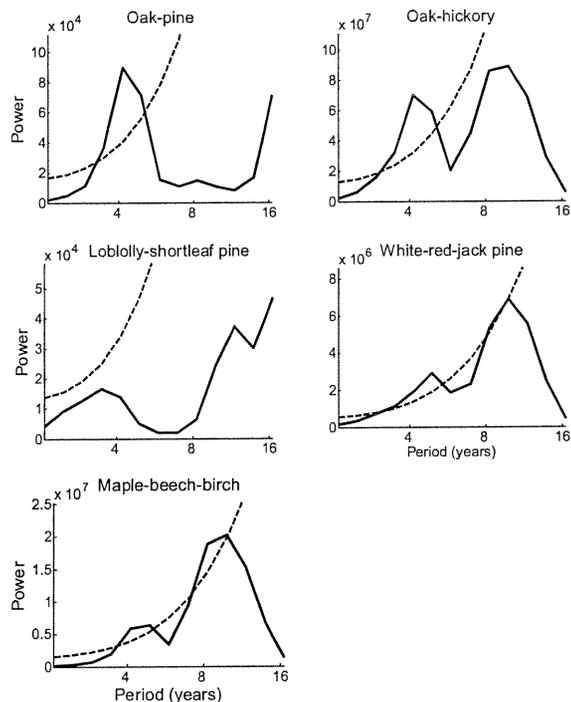


Fig. 3. Forest type-specific wavelet analyses for the $\log_{10}(x+1)$ transformed gypsy moth yearly outbreak probability data. The thick (unimodal and binomial) lines indicate strength of periodicity. Areas above the thin (monotonically increasing) lines indicate significant periodicity.

had outbreaks tending toward 10-yr periodicities, and oak–pine, which had outbreaks tending toward 5-yr periodicities.

The above-described 5-yr periodicities could be the result of two possible patterns: 1) an overall dominant 5-yr periodicity locally within quadrats, or 2) they could be artifacts of aggregating outbreak data across locations (i.e. if two quadrats had 10-yr periodicities that were completely out of phase, then the wavelet analysis of the aggregated data would suggest a dominant 5-yr periodicity). To distinguish between these two possibilities, we performed the following analyses. We focused on all quadrats that had an outbreak between 1979 and 1981, and asked what proportion of these quadrats had subsequent outbreaks in the other dominant and subdominant outbreak peaks, occurring at 5-yr intervals (Fig. 4). If repeating outbreaks were more common after 5 yr than after 10 yr, then this would be evidence that 5-yr periodicities were locally dominant. Alternatively, if repeating outbreaks were more common after 10 yr, then the 10-yr periodicities were more dominant. We found that in two forest types, white–red–jack pine and maple–beech–birch, the 10-yr cycle was strongly dominant at the local scale. In oak–hickory, the 10-yr cycle was dominant, but with evidence for a subdominant 5-yr periodicity at the local scale. In contrast,

Table 1. Mean and 95% CI of the probability of an outbreak per year of the gypsy moth over the 28 yr time series at the 1 by 1 km quadrat scale by dominant forest type group (N = number of 1 by 1 km quadrats; 95% CI was calculated by bootstrapping the data with replacement 1000 times; O–P = oak–pine, O–H = oak–hickory, L–S P = loblolly–shortleaf pine, W–R–J P = white–red–jack pine, and M–B–B = maple–beech–birch).

Forest type	N	No. of outbreaks 28 yr	95% CI
O–P	3464	0.079	[0.077, 0.081]
O–H	100383	0.066	[0.065, 0.066]
L–S P	5743	0.050	[0.049, 0.051]
W–R–J P	17949	0.046	[0.045, 0.046]
M–B–B	144741	0.018	[0.017, 0.018]

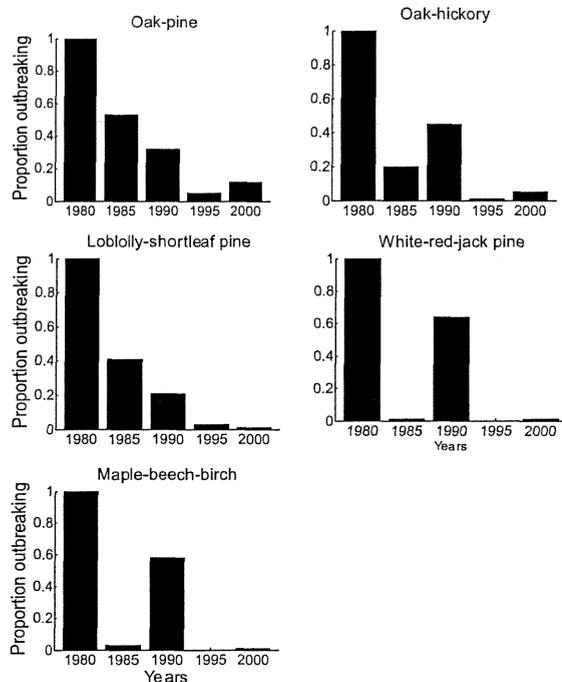


Fig. 4. Of the 1 × 1 km quadrats in each forest type that had an outbreak between 1979 and 1981 (labeled 1980 on the x axis), what proportion of those quadrats also had outbreaks in 1984–1986, 1989–1991, 1994–1996, and 1999–2001 (labeled 1985, 1990, 1995, and 2000, respectively, on the x axis). The sample sizes are n = 917 for oak–pine, n = 31 219 for oak–hickory, n = 987 for loblolly–shortleaf pine, n = 5638 for white–red–jack pine, and n = 9727 for maple–beech–birch.

outbreaks in oak–pine forests were more strongly dominated by a 5-yr periodicity at the local scale. Although no significant periodicity was detected in populations in loblolly–shortleaf pine, results from Fig. 4 suggest that a 5-yr periodicity was stronger than a 10-yr periodicity.

Discussion

The gypsy moth is a generalist herbivore, feeding on over 500 plant species worldwide and over 200 tree species in North America (Liebhold et al. 1995b). Nevertheless, it is widely recognized that most of the stands where outbreaks develop within the gypsy moth's North American range are dominated by *Quercus* spp. (oaks) and/or *Populus* spp. (Bess et al. 1947, Houston and Valentine 1977, Gottschalk 1993, Liebhold et al. 1995b, Davidson et al. 2001). A common finding of these studies is that forest susceptibility is closely related to the proportion of tree species that are highly preferred by gypsy moth larvae. Our results confirm that forests dominated by *Quercus* spp., compared to other species, are highly susceptible to gypsy moth outbreaks (Table 1). In particular, outbreaks were most probable in oak–pine

and oak–hickory forest type groups, and to a lesser extent in pine forest type groups. Liebhold et al. (1994) also found that pine forest type groups, along with oak–pine and oak–hickory, were the most susceptible to gypsy moth outbreaks. Why are pine forest type groups apparently so susceptible to gypsy moth outbreaks when the early instars cannot feed on pine foliage? An answer may lie in the fact that forest type groups form a general classification that encompasses a range of tree species compositions; many of the forest type groups dominated by pines, also include a significant component of oak (Eyre 1980). Thus, the secondary presence of preferred hosts in pine dominated forest types may increase the susceptibility of the forest to defoliation by the gypsy moth.

It has been reported previously that North American gypsy moth outbreaks are periodic at an ca 10 yr cycle (Williams and Liebhold 1995, Liebhold and Kamata 2000, Johnson et al. 2005). Our analyses revealed a more complex dynamic with two significant periodicities, one centered around 4–5 yr and the other centered around 8–10 yr (Fig. 1). Moreover, the periodicities differed among forest type groups, with populations in oak–pine and oak–hickory having significant 4–5 yr periodicities, those in white–red–jack pine and maple–beech–birch having both significant 4–5 yr and 8–10 yr periodicities, and those in loblolly–shortleaf pine lacking any significant periodicity (Fig. 3).

While the most obvious interpretation of these results is that overall periodicity in gypsy moth outbreaks was bimodal, an alternative hypothesis is that all gypsy moth populations were in 8–10 yr cycles, where some peaked around 1980, 1990, and 2000, while the others peaked out of phase (around 1985 and 1995). A similar phenomenon was observed in the epidemic cycles of measles in England in which outbreaks in one area fell out of phase with those in other areas over a period of several years (Grenfell et al. 2001). This alternative hypothesis is consistent with conventional wisdom that gypsy moth outbreaks occur at an 8–10 yr periodicity. This would suggest that the 4–5 yr periodicities detected in oak–pine and oak–hickory forests, and to a lesser extent in white–red–jack pine and maple–beech–birch forest, are artifacts of aggregating outbreak data from multiple sites (all on 8–10 yr cycles, but some peaking on the dominant cycle and the others peaking on the anti-synchronous cycle). The results presented in Fig. 4 suggest that, at the local scale, the 4–5 yr cycle was dominant in oak–pine forest, supporting the bimodality hypothesis. In oak–hickory forests, the 8–10 yr cycle was moderately more prevalent than the 4–5 yr cycle. However, the 8–10 yr periodicity of the gypsy moth in oak–hickory forest was quite strong (though insignificant, Fig. 3), thus, these results are also consistent with the bimodality hypothesis. In contrast, while white–red–jack pine and maple–beech–birch forests had signifi-

cantly bimodal periodicities in aggregated data, Fig. 4 reflects very strong 8–10 yr periodicity at the local level and very little evidence for a 4–5 yr cycle. Yet, Fig. 3 indicates significant 4–5 yr cycles in white–red–jack pine and maple–beech–birch, thus, gypsy moth populations in these forest types may be dominated by two 8–10 yr cycles that are in anti-synchrony. Logistic regression analysis suggested significant forest type differences in periodicity, driven primarily by a stronger 5-yr outbreak periodicity in oak–pine forest compared to a stronger 10-yr periodicity in loblolly–shortleaf pine forest. In whole, the majority of the evidence points toward bimodality in the periodicity in gypsy moth population dynamics in most forest type groups. As a caveat to this interpretation, it should be recognized that these results are based on defoliation data, not species abundance data. With this in mind, an alternative explanation is that all populations are cycling on a 5-yr cycle, but with higher density peaks only every 10 yr and lesser density peaks 5 yr after. In such a scenario, populations in optimal forest types may defoliate the forest during both the high and low density peaks, but those in sub-optimal habitat may reach defoliating population sizes only during the high density peaks every 10 yr. This possibility deserves further scrutiny.

We found that the periodicity of gypsy moth outbreaks varied among forest types. Peltonen et al. (2002) analyzed gypsy moth time series and found geographic variation in population dynamics (as measured by autoregressive parameters in 2nd order linear models fit to similar geographical subset data analyzed here) in North America, and through a simulation model, demonstrated that this variation could reduce synchrony in outbreak dynamics among populations. Variation in periodicity has been reported in a number of natural systems. Previous studies demonstrate geographic changes in periodicity of population cycles of small mammals in Japan and Europe, linking the variability in periodicity to differences and gradients in abiotic factors such as latitude (Bjørnstad et al. 1995), elevation (Bjørnstad et al. 1996), and refugia (Fromentin et al. 1997). In a report with certain similarities to the present study, Volney and McCullough (1994) reported that geographical variation in periodicity of jack pine budworm populations and found that outbreak frequency was positively associated with xeric habitat conditions. Various biotic factors have been proposed to explain variation in outbreak patterns and periodicity of populations as well (Bjørnstad et al. 1998). Geographic transitions in periodicity of the colored fox in Quebec was proposed to be the result of the fox tracking two different prey with cyclical dynamics, the snowshoe hare with a 10-yr cycle and lemmings with a 4-yr cycle (Butler 1951). Grouse populations in Great Britain were reported to cycle with distinctly different periodicities: 3–4 yr in England (reportedly caused to host-parasite

interactions) (Dobson and Hudson 1994, Hudson et al. 1998) and 6–15 yr in Scotland (reportedly caused by social and age-structured interactions) (Moss et al. 1996, Watson et al. 2000). The cause(s) of the latitudinal gradient in periodicity of microtine rodents in northern Europe is unresolved, but some proposed mechanisms include variation in predation (Turchin and Hanski 1997), snow cover (Hansson and Henttonen 1985), and vegetation composition (Hansson 1992). Northern populations of the autumnal moth *Epirrita autumnata*, display periodic oscillations causing widespread defoliation in Fennoscandia but more southerly populations exhibit little periodicity; this gradient has been hypothesized to result in shifts in dominance from specialist to generalist predators from northern to southern latitudes (Klemola et al. 2002). We did not specifically address the effects of a latitudinal gradient on periodicity in gypsy moth outbreaks. However, because the distribution of forest types is certainly related to latitude (Appendix Fig. S1), it could result in spurious correlations between outbreak periodicity and forest type. Our method of using local probabilities of 5- and 10-yr dominant periodicities, rather than global probabilities, in the logistic regression model corrected for such spurious spatial correlations. Thus, we are confident that the relationship between outbreak periodicity of the gypsy moth and forest type is real.

We present correlative data in support of the hypothesis that geographical variation in vegetative composition is associated with variation in gypsy moth outbreak dynamics in North America. The mechanisms responsible for the variation in periodicity of gypsy moth populations across forest types are unclear. The gradation in forest type groups that is associated with the gradation from 5 to 10 yr periodicity appears to correspond to a continuum of forest types found from xeric to mesic habitats. That is, oak–pine forest types are common in dry soils and these were areas where 5-yr periodicity dominated. In mesic sites, where maple–birch–beech and white pine types are typical, gypsy moth populations were dominated by a 10 yr oscillation period. There are numerous reports in the literature that gypsy moth outbreak frequencies tend to be greater on dry sites (e.g. Houston and Valentine 1977). At least one explanation for this relationship is that that small mammal predator communities tend to be lower on dry sites (Smith 1985, Yahner and Smith 1991, Liebhold et al. 2005). Predation by small mammals is considered the single most important factor affecting low-density gypsy moth populations and several studies indicate that variation in small mammal abundance is a primary determinant of when and where gypsy moth outbreaks occur (Campbell and Sloan 1977, Campbell et al. 1977, Elkinton and Liebhold 1990, Liebhold et al. 2000). However, this is the first report indicating that dry sites are characterized by distinctly different outbreak peri-

odicities (5 vs 10 yr). It is unclear how variation in densities of small mammal communities would cause bimodal periodicities in the gypsy moth because there is no evidence for geographic bimodality in small mammal oscillations. Thus, further work is needed to determine whether these differences in outbreak periodicity are indeed related to differences in predator communities or some other factor such as host species composition, other natural enemies, or other habitat characteristics.

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