POPULATION ECOLOGY - ORIGINAL RESEARCH

Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect

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Abstract Recent collapses of population cycles in several species highlight the mutable nature of population behavior as well as the potential role of human-induced environmental change in causing population dynamics to shift. We investigate changes in the cyclicity of gypsy moth (*Lymantria dispar*) outbreaks by applying wavelet analysis to an 86-year time series of forest defoliation in the northeastern United States. Gypsy moth population dynamics shifted on at least four occasions during the study period (1924–2009); strongly cyclical outbreaks were observed between ca. 1943–1965 and ca. 1978–1996, with noncyclical dynamics in the intervening years. During intervals of cyclical dynamics, harmonic oscillations at cycle lengths of 4–5 and 8–10 years co-occurred. Cross-correlation analyses indicated that the intensity of suppression efforts (area treated by insecticide application) did not significantly reduce the total area of defoliation across the region in subsequent years, and no relationship was found between insecticide use and the cyclicity of outbreaks. A gypsy moth population model incorporating empirically based trophic interactions produced shifting population dynamics similar to that observed in the defoliation data. Gypsy moth cycles were the result of a high-density limit cycle driven by a specialist pathogen. Though a generalist predator did not produce an alternative stable equilibrium, cyclical fluctuations in predator density did generate extended intervals of noncyclical behavior in the gypsy moth population. These results suggest that changes in gypsy moth population behavior are driven by trophic interactions, rather than by changes in climatic conditions frequently implicated in other systems.

Keywords Gypsy moth · *Lymantria dispar* · Generalist predator · Insecticide · Nonlinear dynamics

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Introduction

Population cycles are displayed across a broad variety of taxa, including large mammals, small mammals, birds, and insects (Berryman 2002). Population cycles are, by definition, regular fluctuations in abundance, yet cycles may not persist in natural populations. Recently observed changes in the dynamics of the larch budmoth provide perhaps the clearest example of a temporal shift in the cyclicity of population dynamics. Esper et al. (2007) reported that highly regular cycles (mean cycle length = 9.3 years) occurred for 1,100+ years but abruptly ended in recent decades. Similar collapses of population cycles have occurred recently in several other species as well, presumably as a result of climate change (Ims et al. 2008). Investigating shifts in the cyclicity of field populations requires the availability of unusually long time series of population abundances as well as consideration of the effects of changing environmental factors.

Nonlinear theory predicts that drastic or long-term shifts in conditions (abiotic or biotic) are not necessary to produce dramatic shifts in population behavior. Simple nonlinear population models can display a variety of different modes of dynamics, including stable abundances, cyclical and noncyclical fluctuations, and chaos (Rohani et al. 1994; Costantino et al. 1995; Dennis et al. 1997; Hastings 2004). In nonlinear systems, a rapid shift in population behavior may come about in two different ways. First, a minor change in the value of a model parameter (e.g., population growth rate) may cause a shift between different modes of population behavior (May 1974; Hassell et al. 1976; Rohani et al. 1994), a phenomenon known as a bifurcation. Second, the presence of multiple attractors (e.g., equilibria, limit cycles, strange attractors) can lead to abrupt changes in population behavior. In these cases, perturbations to the system (e.g., stochastic effects) can cause a population's trajectory to jump from one attractor to another (Henson et al. 1998; Bauch and Earn 2003; Dwyer et al. 2004). Empirical support for these theoretical predictions stems largely from studies done on laboratory populations of flour beetles (*Tribolium*) (Costantino et al. 1995; Dennis et al. 1997; Henson et al. 1998). Henson et al. (1998), for example, showed that shifts in the cyclicity of *Tribolium* beetles resulted from stochastic jumps between basins of attraction.

North American populations of the gypsy moth (*Lymantria dispar*) exhibit complex cyclical behavior. In most years, gypsy moths occur at such low densities that life stages are difficult to find, but occasional eruptive population growth leads to intense defoliation of forests over large areas (Liebhold et al. 2000). The time interval between such outbreaks is somewhat irregular (Liebhold et al. 2000; Fig. 1), but spectral analysis of gypsy moth time series provides statistical evidence of both a five-year and a ten-year cycle (Johnson et al. 2006a; Haynes et al. 2009b). Previous formal analyses (Williams and Liebhold 1995; Johnson et al. 2006a; Haynes et al. 2009b) have used ~15–30-year time series, and did not assess changes in population behavior through time. Analysis of time series that are several times longer than the length of gypsy moth outbreak cycles would be required to evaluate the extent of the temporal variation in cycling.

Dwyer et al. (2004) hypothesized that the irregularity of gypsy moth outbreaks may be the result of the presence of two attractors: a high-density limit cycle generated by host-pathogen interactions with the specialist *L. dispar* nucleo-polyhedrosis virus (LdNPV), and a stable, low-density equilibrium caused by small-mammal predators. However, the stability of the low-density node is uncertain given empirical evidence indicating predator-induced mortality is positively density dependent, and consequently destabilizing (Elkinton et al. 2004). Under this assumption, predation
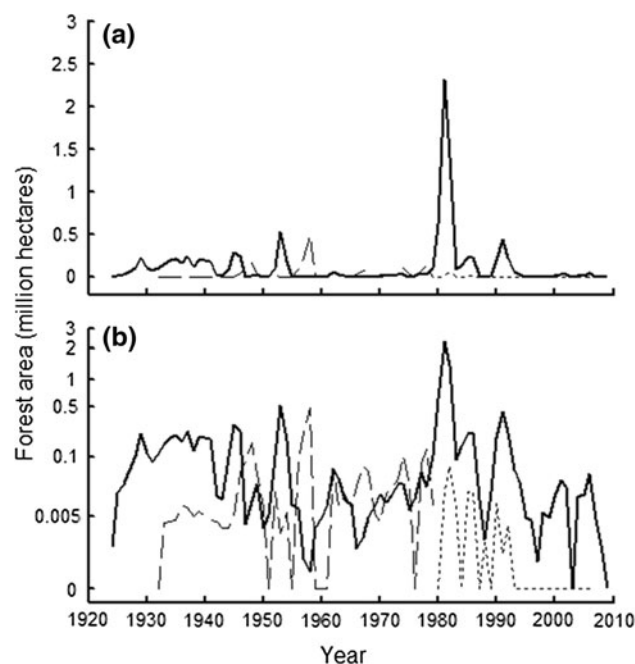

Fig. 1 **a** Raw and **b** transformed time series of forest area defoliated by gypsy moths (*Lymantria dispar*) from 1924 to 2009 across Maine, Massachusetts, New Hampshire, and Rhode Island (*solid line*), and forest area treated with pesticides in gypsy moth suppression efforts. The pre-1980 suppression series is the total area within the U.S. that was treated with pesticides (*dashed line*). The more recent (1980–2006) suppression time series is specific to the four states from which the defoliation series was derived (*dotted line*)

would generally produce a weak Allee effect (reduced growth) in low-density gypsy moth populations, but could cause a strong Allee effect (negative growth) when predation rates are high (Bjørnstad et al. 2010). Given evidence that populations of the gypsy moth's chief predator (the white-footed mouse, *Peromyscus leucopus*) exhibit high-amplitude cycles (Elias et al. 2004; Wang et al. 2009), switching between weak and strong Allee effects may occur frequently. This switching might produce temporal shifts in gypsy moth population behavior, potentially explaining why the interval between gypsy moth outbreaks has historically been somewhat irregular. However, the influence of temporal variation in Allee effect strength on shifts in gypsy moth cyclicity has not been explored.

The gypsy moth is native to Eurasia. During its North American history, gypsy moth populations have been subjected to sometimes massive aerial applications of pesticides, largely targeted at suppressing outbreaks (Liebhold and McManus 1999). For example, chemical insecticides (e.g., DDT) were annually applied over millions of hectares of forest lands in the US during the 1940s and 1950s. More recently, aerial suppression of gypsy moth outbreaks continues to be practiced on a smaller scale, largely with the use of microbial insecticides. Given the scale of historical applications and the potential sensitivity

of nonlinear system behavior, aerial spraying practices might play a role in shaping changes in gypsy moth population dynamics.

In this paper, we use wavelet analysis to investigate the temporal variability in the cyclicity of gypsy moth populations in North America. This assessment is based on an 86-year record of forest defoliation, the longest time series ever used in a formal analysis of gypsy moth population behavior. We then evaluate alternative hypotheses about the causes of changes in population dynamics through time. We explore whether suppression programs alter gypsy moth population behavior, and use an empirically derived population model to determine if temporal variation in predation pressure can cause temporal shifts in cyclicity.

Methods

Gypsy moth defoliation time series

In each state where the gypsy moth has become established, government agencies conduct annual surveys of defoliation. State-level data compiled from these surveys (U.S. Forest Service Gypsy Moth Digest; http://www.na.fs.fed.us/fhp/gm/defoliation) currently span 86 years (1924–2009) and represent the longest available time series on gypsy moth activity in North America. By 1924, only four states—Massachusetts, New Hampshire, Rhode Island, and Maine—had gypsy moth populations established throughout most or all of the state. We limited our analysis of gypsy moth dynamics to defoliation data from these four states to avoid artifactual increases in defoliated area associated with range expansion, as well as the initial synchronization that has been observed in gypsy moth populations during the ten years following establishment (Bjørnstad et al. 2008). Defoliation time series from these four states cannot be considered completely independent because outbreaks are synchronous across distances of up to ~900 km (Williams and Liebhold 1995; Haynes et al. 2009a). Therefore, the number of hectares defoliated in each state were summed into a single time series. Total area of defoliated forest can be considered a proxy for gypsy moth density, since defoliation area is correlated with the density of gypsy moth egg masses through time (Williams et al. 1991; Liebhold et al. 1993).

We examined the cyclicity of gypsy moth defoliation using wavelet analysis. Wavelet analysis is similar to Fourier analysis in that both are used to extract frequency information from a signal, but wavelet analysis has the advantage that it can be used to detect changes in the frequency and amplitude of oscillations in the signal through time (Torrence and Compo 1998). The continuous wavelet transform is computed by sliding wavelets (zero-mean mathematical functions exhibiting oscillations that are localized in time; Farge 1992; Torrence and Compo 1998) of varying temporal scale across a time series to measure how well wavelets of different widths approximate the actual data (Torrence and Compo 1998). The frequency of oscillations in the data is then estimated based on the relationship between the width and the cycle length of the wavelet function. Temporal changes are investigated by computing a series of time-localized power spectra for each of N points in time, where N is the number of observations in the time series (Torrence and Compo 1998). We visualized changes in the frequency and cyclicity of oscillations through time by generating a contour plot of the local wavelet power spectra.

We tested for the presence of significant cyclicity in the defoliation time series using a Monte Carlo simulation experiment outlined by Cazelles et al. (2007), where the power spectrum of the actual time series differed from that of a red-noise process, a random walk with first-order temporal autocorrelation. This results in a conservative test of whether cyclical behavior is present in the actual time series, because it avoids spurious significant results caused by temporal autocorrelation (Cazelles et al. 2007). We generated 1,000 simulated time series using a first-order autoregressive model, with the autoregressive and error terms estimated directly from the defoliation time series. We then compared the power values from the actual time series to the distribution of power values obtained from the 1,000 simulated time series (at all points in the time-scale plane). A power value was deemed to be significantly higher than expected by chance if it fell above the 95th percentile of the simulated values.

We conducted the wavelet analyses using a Matlab package developed by Bernard Cazelles (available at http://dl.getdropbox.com/u/192975/Wavelets_EETS.zip), modified to correct for a bias inherent to traditional wavelet analysis [Liu et al. 2007, see the Electronic supplementary material (ESM), online resource 1]. Prior to performing wavelet analysis, a power transformation $f(x) = x^t$, with $t = 0.2$, was used to normalize the distributions of observations (Sardeshmukh et al. 2000). More traditional square-root and logarithmic transformations were not able to remove strong positive skews, and power transformations are appropriate for positive variables bounded on the left (Williamson and Gaston 1999). Furthermore, the actual and red-noise time series were standardized to have means of zero and standard deviations of one (Torrence and Compo 1998).

Insecticide use effects

Long-term data (1934–2009) on insecticide use in gypsy moth suppression programs in the United States were used

to examine relationships between suppression effort, level of defoliation, and outbreak cyclicity. We used two sources of data on insecticide use: (1) an older (1934–1979) time series (on file with U.S.D.A. Forest Health Protection, U.S. Forest Service in Morgantown, WV, USA) of total annual forested areas across the entire northeastern United States treated with insecticides as part of gypsy moth suppression efforts, and (2) a newer (1980–2006) time series which records area treated for suppression by state (U.S. Forest Service Gypsy Moth Digest, http://www.na.fs.fed.us/fhp/gm/suppression). For the newer data, we only used insecticide data from the four states corresponding to the defoliation data, but this was not possible with the older suppression data. Several different chemical (e.g., DDT, carbaryl, diflubenzuron) and biological (*Bacillus thuringiensis*, gypsy moth nucleopolyhedrosis virus) insecticides have been used on gypsy moths throughout the history of their invasion of North America (Liebhold and McManus 1999). Rather than try to isolate the effects of individual insecticides, we evaluated the effects of the overall suppression effort measured as the total annual area treated with any insecticide. To assess potential instantaneous and lagged effects of insecticides on defoliation and outbreak cyclicity, we computed Pearson cross-correlations for lags of −5 to 5 years. When performing cross-correlations, serial correlation (e.g., regular fluctuations) in the time series can lead to the detection of spurious relationships (Chatfield 2004). To avoid bias caused by autocorrelation and cyclical oscillations in the time series, statistical significance was assessed using generalized least-squares regression (Fox 2002). Autocorrelation in the regression errors was accounted for using an autoregressive model for the errors. For each analysis, the order of the autoregressive model was chosen based on AIC values (the order ranged from 1 to 3). Prior to these analyses, all time series were transformed to be stationary processes (Chatfield 2004). Variances were made approximately independent of the mean using the fifth-root power transformation described previously, and then linear trends were removed from the time series.

Gypsy moth population model

We studied a gypsy moth population model to determine if temporal variation in gypsy moth population behavior could be generated through trophic interactions. Our model incorporated interactions between a gypsy moth population and its major sources of mortality during development: a pathogen (LdNPV) during the larval stage, and predation during the pupal stage. LdNPV is a major contributor to the collapse of gypsy moth outbreaks, as it can cause high larval mortality in high-density populations (Leonard 1981; Dwyer et al. 2000). In contrast, generalist predators,

particularly *P. leucopus*, are the largest source of mortality in low-density gypsy moth populations and are thought to suppress the regrowth of populations following the collapse of outbreaks (Campbell and Sloan 1977; Elkinton et al. 1996). A model capturing these interactions was first presented in Dwyer et al. (2004), and subsequent studies have made three major modifications that we incorporated. First, in the original model mortality from all sources occurred simultaneously, while subsequent versions have been modified to reflect the stages of gypsy moth development when these interactions occur (Bjørnstad et al. 2010; Haynes et al. 2012). Second, the response of predators to prey density has been changed from a type-III to a type-II functional response (Bjørnstad et al. 2010; Haynes et al. 2012). Third, we compare simulations using constant predator density (as in Haynes et al. 2012) to those with a density that varies in time (as in Bjørnstad et al. (2010), though we use a more realistic, empirically based model). In contrast with previous studies (Bjørnstad et al. 2010; Haynes et al. 2012), our analysis emphasizes temporal variation of gypsy moth population dynamics over mean spectral characteristics.

In our model, the initial density of female larvae ($\tilde{N}_t$) hatching in the spring is

$$\tilde{N}_t = \lambda N_{t-1} \tag{1}$$

where λ and N_{t-1} are the mean fecundity and density of adult female moths in the previous year, respectively. Newly hatched larvae are exposed to LdNPV virions remaining in the environment from previous years (Doane 1975), and the epizootic progresses rapidly compared to the development of the gypsy moth until the gypsy moth enters the pupal stage (Leonard 1981; Dwyer et al. 2000). Thus, the fraction of larvae killed by disease in year t, $I(\tilde{N}_t, Z_t)$, is a function of both initial larval density and the initial virion density (Z_t) in the environment. As in Dwyer et al. (2004), $I(\tilde{N}_t, Z_t)$ was found by solving the implicit equation

$$1 - I(\tilde{N}_t, Z_t) = \left[1 + \frac{v\tilde{N}_t}{\mu k}I(\tilde{N}_t, Z_t) + \rho Z_t\right]^{-k}, \tag{2}$$

where μ is the rate at which cadavers lose infectiousness, and the ratio ρ relates the susceptibility of hatchlings to that of later-stage larvae. Heterogeneity in larval susceptibility to infection follows a gamma distribution with a mean of v and a shape parameter of k (Dwyer et al. 2000). The initial pathogen density of the following year is

$$Z_{t+1} = \phi\tilde{N}_t I(\tilde{N}_t, Z_t), \tag{3}$$

where ϕ is a constant combining the number of virions produced and the overwinter survival rate (Dwyer et al. 2004). To prevent LdNPV from going extinct in the system during extended intervals of low gypsy moth density, Z_t

was given an arbitrary minimum value of 10^{-10}. Population dynamics were not sensitive to the minimum value used due to the rapid response of Z_t to high $\tilde{N}_t$ (not shown). For the population growth and disease model parameters, we used values that Dwyer et al. (2004) calculated from a combination of lab and field experiments. These values are $\lambda = 74.6$, $\mu = 0.32$, $\rho = 0.8$, $\upsilon = 0.9$, $k = 1.06$, and $\phi = 21.33$.

Larvae surviving the epizootic become pupae, which are subject to predation, largely by mammalian predators. The fraction of pupae eaten in a given year depends on both initial pupal (N_t') and predator (P_t) density, as related through the predation functional response. Most empirical evidence suggests that the proportion of a gypsy moth population consumed by small mammal predators decreases monotonically as the gypsy moth population density increases (Elkinton et al. 1996, 2004; Grushecky et al. 1998; but see Schauber et al. 2004). This implies that predation on gypsy moth pupae follows a type-II functional response. Therefore, we followed the form of the type-II response developed in Haynes et al. (2012), where the density of female pupae surviving to adulthood is

$$N_t = N_t' \exp\left(-\frac{cdP_t}{N_t' + d}\right)e^{\varepsilon_t}. \tag{4}$$

The stochastic term ε_t is discussed below. The parameters c and d determine (but are not equal to) the fraction of pupae killed at low gypsy moth density and the pupal density at which half of the maximum fraction killed is realized (half-saturation point), respectively.

Predation following a type-II response produces an unstable equilibrium at a low pupal density, representing the Allee threshold. The density at which the Allee threshold occurs depends on current mortality due to both predation and disease. However, given that predator-induced mortality is generally dominant at low gypsy moth densities, a simple analytical estimate of the Allee threshold (N_A') can be found by ignoring mortality due to disease. N_A' is calculated by assuming $I(\tilde{N}_t, Z_t) = \varepsilon_t = 0$, substituting Eq. 4 into Eq. 1, and setting $\tilde{N}_{t+1} = N_t'$, giving

$$N_A' = d\left(\frac{cP_t}{\ln\lambda}\right). \tag{5}$$

This value can be used to classify the contribution of predation to the gypsy moth population growth rate at low densities. That is, predation causes a strong Allee effect if $N_t' < N_A'$, and a weak Allee effect if $N_t' > N_A'$. When there is substantial disease mortality in a low-density gypsy moth population (often immediately following an outbreak), the Allee threshold is shifted to a higher density (see Fig. 3 in Bjørnstad et al. 2010). N_A' is a conservative estimate, as disease mortality could result in a missed strong Allee

effect, but will not produce a false positive. Further, setting $N_A' = 0$ in Eq. 5 allows the minimum predator density able to cause a strong Allee effect (P_A) to be calculated. If $P_t < P_A$, N_A' is negative, and predation can only cause a weak Allee effect, regardless of pupal density.

To examine how the cycling of predator populations might influence gypsy moth population behavior, we compared simulations with a constant predator density to those using a cyclical predator density model. Densities of the gypsy moth's primary predator, *P. leucopus*, are not strongly influenced by densities of gypsy moth pupae (Elkinton et al. 1996). Thus, predator density in or models was independent of gypsy moth density. In the constant predator model ($P_t = P_{\text{const}}$ for all t), stochasticity was applied in Eq. 4, with ε_t representing normally distributed noise. Since the number of adults leads directly to the number of larvae in the following year, this could be considered variation in fecundity. Assigning ε_t a standard deviation of 0.55 produced gypsy moth population fluctuations across four orders of magnitude at moderate predator densities, approximating fluctuations observed in natural populations (Berryman 1991). The cyclical predator model is based on an empirical study of *P. leucopus* populations in Maine, USA, from 1984 to 2005 (extended data from Elias et al. 2004). Among several potential statistical models, Elias et al. (2004) found that a second-order autoregressive model best fit the data. Therefore, we generated the predator density using the same model:

$$\log(P_t) = \alpha_0 + \alpha_1 + \log(P_{t-1}) + \alpha_2 \log(P_{t-2}) + \xi_t. \tag{6}$$

Using the Elias et al. (2004) time series, we calculated the autoregressive parameters for average density and the direct and indirect density dependence as $\alpha_0 = 1.56$, $\alpha_1 = 0.456$, and $\alpha_2 = -0.464$, respectively. The term ξ_t represents normally distributed stochastic variation with a mean of zero and a standard deviation of 0.954, also estimated from the data. These values produce a predator population cycle of approximately five years (Royama 1992). For this version of the model, we set $\varepsilon_t = 0$ in Eq. 4, to avoid inflating variability in gypsy moth population dynamics through the inclusion of multiple sources of stochasticity.

The predation functional response (Eq. 4) was parameterized to integrate the cyclical predator model (Eq. 6), while maintaining the empirically derived characteristics used in previous studies. We used the same N_t' predation half-saturation point as Dwyer et al. (2004), and set predation rates at high P_t based on the distribution of values produced by Eq. 6 and parameters from Bjørnstad et al. (2010). Parameters c and d were then calculated following Haynes et al. (2012). As described in detail in the ESM (online resource 2), we found that a functional response using parameters $c = 0.3195$, $d = 0.0454$ produced

predation mortality patterns similar to those found in nature. These parameters give $P_A = 13.5$. The constant predator model also used the same functional response, and predation pressure was controlled by varying P_{const} among simulations.

We ran simulations for 100 years, similar to the 86-year length of the defoliation data. After the completion of a simulation, temporal variation in the cyclicity of the gypsy moth population was assessed with wavelet analysis of larval density (the stage responsible for defoliation). We examined the resulting wavelet spectra and observed the frequency of "gaps" in cyclical behavior, which we defined as a break of five or more years in significant cyclicity. The timing of these gaps was compared with the time series for all species, stochastic effects in those years, and the occurrence of strong Allee effects. Prior to wavelet analysis, larval densities were transformed using the Box–Cox technique (Box and Cox 1964) to improve normality, and were then standardized to zero mean and a standard deviation of 1. Initial conditions for all species were randomly selected in the cyclical predator simulations, while in the constant predator we conducted simulations for a range of P_{const} values. To reduce the impact of the initial conditions, all simulations had a 100-year "burn-in" period during which no data were recorded.

Results

Defoliation time series

Based on the annual defoliation records, the gypsy moth exhibited high-amplitude oscillations in abundance throughout much of the study period (1924–2009; Fig. 1). However, defoliation remained at relatively low levels during two extended intervals, first from the mid-1950s to mid-1970s, and again after the mid-1990s. The area defoliated annually during these intervals of low gypsy moth activity (1955–1975 and 1994–2009) was, on average, only 6.7 % of the area defoliated annually during all other years.

The cyclicity of defoliation varied considerably through time (Fig. 2). Defoliation levels fluctuated with significant cyclicity during three disjunct time intervals: ca. 1943 to 1965, ca. 1978 to 1996, and after ca. 2002. How long this behavior persisted beyond 2002 cannot be determined given the recentness of this event. During each of the 1943–1965 and 1978–1996 intervals of cyclical dynamics, approximately three complete cycles are apparent. During substantial portions of the two main occurrences of cyclical behavior, from ca. 1943 to 1965 and ca. 1978 to 1996, the contour plot indicates that power peaked at two different cycle lengths, with the longer cycle roughly twice as long as the shorter cycle (Fig. 2). The shorter cycle was often
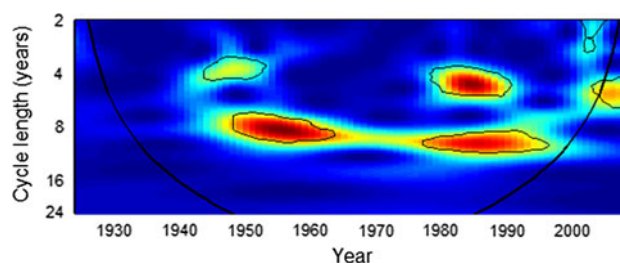

Fig. 2 Temporal profile of cyclical behavior of gypsy moth populations, as measured by forest defoliation. *Red* areas within the plot indicate high power and *blue* areas indicate low power. The *thin lines* enclose areas of the timescale plane where the power values are significantly higher than expected by chance. Power values were deemed significant if they fell above the 95th percentile of power values derived from 1,000 simulations of a red-noise process (Cazelles et al. 2007). The *thicker curved lines* indicate the cone of influence, power values outside these lines are considered suspect because errors may occur near the ends of the time series (Torrence and Compo 1998)

3.5–5 years long, while the longer cycle was 7–12 years long. At other times, however, there was just one strong peak in power, e.g., from ca. 1952 to 1965.

Insecticide effects

From 1934 to 1979, there was a slight trend for defoliated area to decrease with increasing insecticide application area 0–3 years after insecticide use (lags 0 to +3 in Fig. 3a); however, these correlations were not significant. Defoliated area was significantly correlated with insecticide use at only one of the examined lags; insecticide use was positively correlated with defoliation four years in the past (lag −4 in Fig. 3a). With the recent (1980–2006) suppression data, which was specific to the four states of interest, none of the correlations between insecticide application area and defoliated area were significant (Fig. 3b). The strength of cyclical behavior (maximum wavelet power) of defoliation was not correlated with insecticide application area at any of the examined lags for either set of data (Fig. 3c, d).

Gypsy moth population model

In the population model with constant predator density, a major effect of increasing P_{const} from 0 towards $P_A = 13.5$ was to increase the length of gypsy moth outbreak cycles from approximately 6 to 28 years. Over the same range, the size of fluctuations in gypsy moth density increased from four to seven orders of magnitude. Harmonic oscillations were consistently produced when $P_{const} > 11$, and gaps in cyclicity were observed when $P_{const} > 12$. For example, simulations with $P_{const} = 12.25$ produced harmonic oscillations at cycle lengths of ~ 8 and ~ 16 years, and gaps in
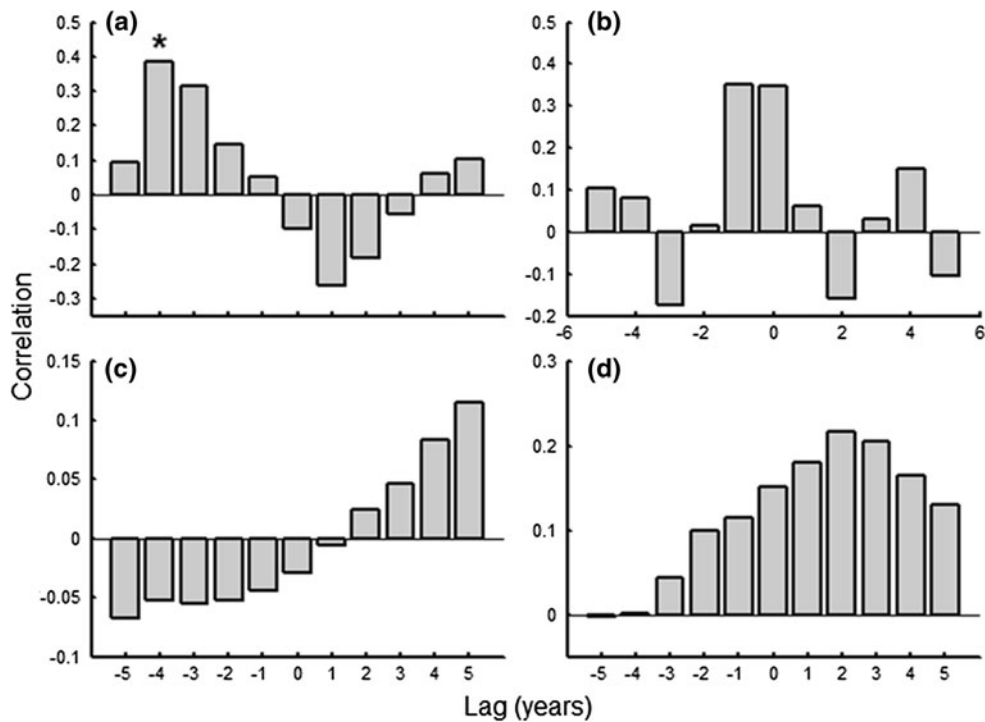
Fig. 3 Cross-correlations between the area treated with insecticide and (**a**, **b**) area defoliated and (**c**, **d**) and the strength of cyclical behavior (maximum power) at lags of −5 to 5 years after the insecticide was applied. Separate analyses were conducted on the (**a**, **c**) pre-1980 data, where the suppression data is derived from throughout the gypsy moth's entire range in the United States, and (**b**, **d**) the 1980–2006 data specific to the states (MA, ME, NH, and RI) corresponding to the defoliation data. *Asterisks* indicate correlations that are significant at the $\alpha < 0.05$ level (significance was determined using generalized least squares regressions to protect against bias caused by serial correlation present in the time series; Fox 2002). All time series were transformed to improve normality and detrended before analysis

cyclicity of at least five years were observed in 39 out of 100 simulations (Fig. 4a). During extended intervals at low gypsy moth density following the crash of an outbreak, poor fecundity (negative stochastic effects) could further reduce the population density and delay the next outbreak (Fig. 5). Harmonic oscillations were produced in two ways. First, stochastic effects could produce what appears to be a cycle at low gypsy moth density, which was then magnified by the transformation of the time series (e.g., year ∼178 in Figs. 4a, 5). Alternatively, the nonsinusoidal shape of the outbreak cycle could create harmonics (Chatfield 2004), which generally showed a high power of subharmonic cyclicity centered around the more deterministic peak and falling phases of the outbreak (e.g., years ∼129–137 in Figs. 4a, 5). When $P_{const} > P_A$, repeated strong Allee effects drove gypsy moth populations to extinction.

With a cyclical predator population, the gypsy moth population exhibited gaps between the occurrences of significant cyclicity lasting for at least five years in 71 out of 100 simulations. When they occurred, gypsy moth cycles exhibited a ∼6–8 year cycle length (Fig. 4b). Examination of the time series (Fig. 6) indicates that time intervals of significant cyclicity corresponded to consecutive gypsy moth outbreaks driven by the delayed density-
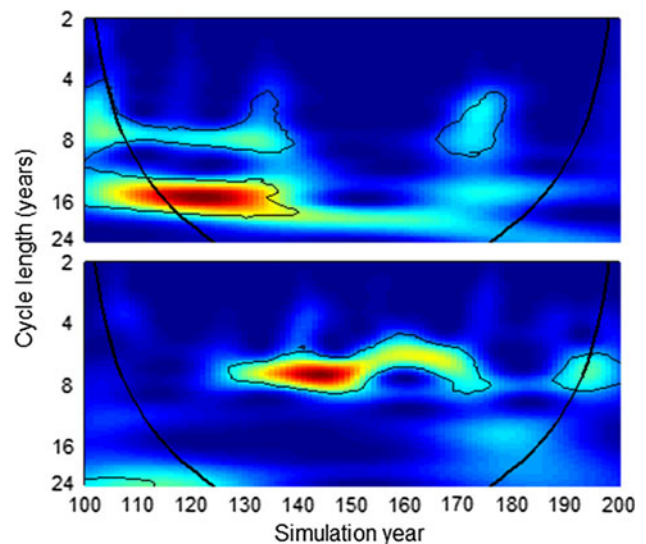

Fig. 4 Sample wavelet spectra showing the temporal variation in the cyclicity of gypsy moth larval populations generated by the simulation model. **a** The constant predator model, with $P_{const} = 12.25$, produced subharmonic oscillations at cycle lengths of ∼8 and ∼16 years from years ∼100 to 140. Oscillations at the ∼8 year cycle length were also present from years ∼168–178. **b** The fluctuating predator model produced cycle lengths of between six and eight years from years ∼125–175, and again after year 190
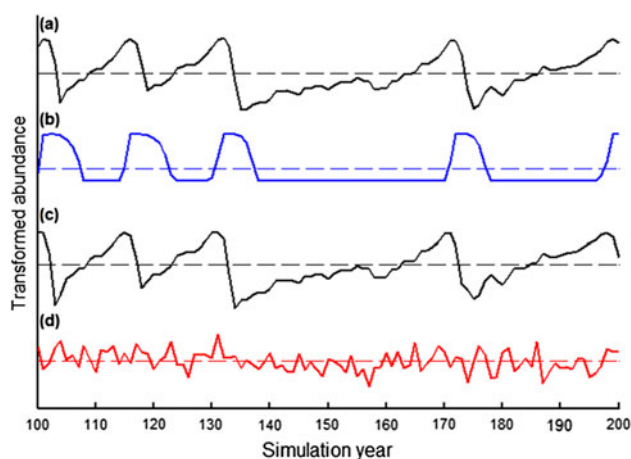
Fig. 5 Time series of transformed species densities and fecundity for the gypsy moth population model with constant predator density. These time series correspond to the simulation presented in Fig. 4a. The lines correspond to (*a*) initial gypsy moth larval density ($\tilde{N}_t$), (*b*) virion density (Z_t), (*c*) pupal density (N_t'), and (*d*) the stochastic effect on gypsy moth fecundity (ε_t). The species-density time series were transformed to improve normality using the Box–Cox technique, and then standardized to have a zero mean and a standard deviation of one

Fig. 6 Time series of transformed species densities produced by the simulation model with a cyclical predator, for the same simulation presented in Fig. 4b. As in Fig. 6, the top three time series represent (*a*) $\tilde{N}_t$, (*b*) Z_t, and (*c*) N_t'. However, here (*d*) represents predator density (P_t). To improve normality, the P_t time series was log transformed, while the Box–Cox transform was applied to $\tilde{N}_t$, Z_t, and N_t' distributions. The mean of each time series (*horizontal dashed line*) is provided for reference. The *vertical dashed lines* indicate years in which predation caused a strong Allee effect

dependent effects of LdNPV on larvae. Initial strong Allee effects occurred when high P_t coincided with the falling phase of an outbreak cycle, as pupal densities were low due to disease-driven larval mortality earlier in the year (Fig. 6). A single strong Allee effect caused only a slightly longer cycle length (e.g., years 141 and 150 in Figs. 4b, 6). Time intervals of noncyclical population behavior were created by repeated strong Allee effects (e.g., years 105–125 and 175–190 in Figs. 4b, 6).

Discussion

We found evidence that in North America, gypsy moth population behavior shifted through time on at least four occasions during the twentieth century. The gypsy moth appeared to switch between cyclical and noncyclical behavior in ca. 1943, 1965, 1978, 1996, and possibly in 2002. Noncyclical behavior generally occurred when density stayed low for an unusually long time (e.g., the mid-1960s to late 1970s). Additionally, there was a shift between cycling at one and two cycle lengths in 1948, 1954, 1980, and 1990. This rate of switching is markedly higher than that reported in some forest insect systems. For example, reconstructed time series of larch budmoth outbreaks indicate that budmoth populations oscillated with a very regular cycle length over 1,100 years until the series became noncyclical in recent decades (Esper et al. 2007). Other tree-ring reconstructions of outbreak histories have produced mixed results. For instance, the population
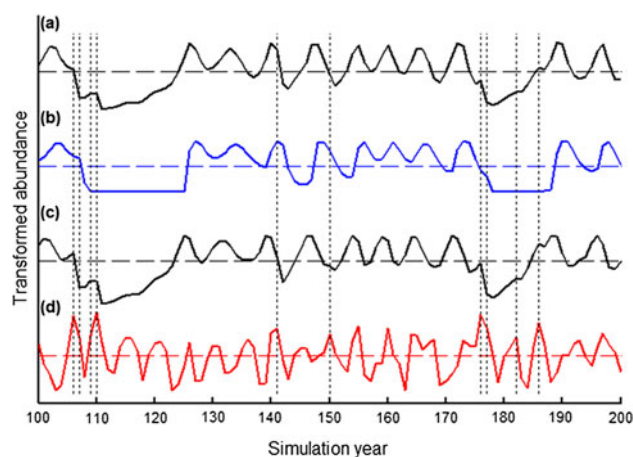
dynamics of the spruce budworm in Eastern Canada have been quite stable for the past several centuries, with outbreaks every 35–40 years (Royama 1992; Boulanger and Arseneault 2004), though isolated instances of unusually long intervals have been observed (Royama 1992). Outbreaks of western spruce budworm and Pandora moth have occurred at fairly regular intervals, but as in the gypsy moth, unusually long time intervals of little or no activity have been reported in both species (Swetnam and Lynch 1993; Speer et al. 2001).

We found little evidence supporting the hypothesis that regional gypsy moth population dynamics are driven by the extent of insecticide applications. We did find a significant lag correlation between defoliation and insecticide use four years later in the pre-1980 data, likely as a result of regional outbreaks triggering large aerial spraying efforts in subsequent years. In one of the few comprehensive analyses of an operational gypsy moth suppression program, Liebhold et al. (1996) found that aerial spraying, while killing a large fraction of gypsy moths in the year of treatment, did not have any detectable effect on post-treatment egg mass densities. This may be due to the fact that the area treated with pesticides is often much smaller than the total size of the outbreak, though this was not the case from 1945 to 1975, when the area treated annually was proportionally large relative to the area defoliated annually (Fig. 1). As is the case in many other forest insect species, the dynamics of gypsy moth populations are synchronous over hundreds of kilometers, and this linkage may explain, in part, the lack of influence that localized aerial spraying has on regional dynamics.

In the original version of the gypsy moth population model, the generalist predator was assumed to exist at a constant population level and exhibit a type-III functional response to changes in gypsy moth density (Dwyer et al. 2004). Dwyer et al. (2004) found that shifts in gypsy moth population behavior could be explained by stochastic switching between a high density limit cycle (due to moth–pathogen interaction) and a locally stable, low-density equilibrium (due to predation). Using a more realistic type-II functional response, both versions of the model presented here (constant predator density or cyclical predator) produced the same type of behavior, despite the lack of a stable, low-density equilibrium. However, the variation in cyclicity was produced in a slightly different manner in each version of our model. For most predator densities used in the constant predator model, the unstable node representing the Allee threshold was located at negative gypsy moth pupal density. Therefore, predation could only cause a weak Allee effect, regardless of pupal density. However, as we increased predator density between simulations, the Allee threshold increased towards zero and predation-induced mortality increased. This reduced the lowest gypsy moth densities reached and also decreased growth at low density (as in Bjørnstad et al. 2010; Haynes et al. 2012). With the expected population growth rate reduced to a very low level, stochasticity in fecundity dominated the growth process and sometimes led to short intervals of noncyclical gypsy moth population behavior. In the cyclical predator model, changes in gypsy moth population behavior were mediated by the independent predator density cycles and the resulting changes in the Allee threshold. Peaks in predator density had little effect on gypsy moth populations unless they occurred during a trough in the gypsy moth–pathogen cycles. Here, high predation rates could cause a strong Allee effect, further reducing gypsy moth population density. If predator density was generally high in subsequent years, predation could cause a strong Allee effect frequently enough to hold the gypsy moth at low population densities and cause intervals of noncyclical behavior. Several years of low predator density released gypsy moth populations, and outbreak cycles resumed.

Though both versions of the gypsy moth population model produced shifts in population behavior, the constant predator density version produced noncyclical behavior less frequently, and only when the gypsy moth populations had unrealistically long cycle lengths. Therefore, it appears that fluctuations in predator density best explain the shifts between cyclical and noncyclical dynamics observed in the defoliation time series. The interactions observed in this model fit with empirical observations, as populations of the gypsy moth's most important predator, *P. leucopus*, are often cyclical (Elias et al. 2004; Wang et al. 2009), and changes in *P. leucopus* density are associated with changes

in pupal predation rates (Elkinton et al. 1996). Further supporting our hypothesis that the timing of interactions between species is important, *P. leucopus* populations in Maine (synchronous up to 700 km; Haynes et al. 2009a) were high in 1994–1995 and low in 1999–2000 (see Fig. 2 in Elias et al. 2004), corresponding to an end and a beginning of cyclical behavior in the defoliation data, respectively (Fig. 2).

One inconsistency between the population dynamics produced by the cyclical predator density model and those observed in defoliation data is that the model generally did not produce cyclical behavior at multiple period lengths. The constant predator model did produce a spectral signal of subharmonic oscillations, either as a result of stochastic effects at low density (magnified by transformation of the time series) or due to the nonsinusoidal character of the outbreak cycles (Chatfield 2004). Either of these effects could have occurred in the defoliation time series, but this does not appear to be the case. While the power at each cycle length is nearly constant in the defoliation data, subharmonic oscillations generated by the constant predator model are much weaker than oscillations at the main cycle length. The mechanisms generating the subharmonic oscillations in nature are still uncertain. The appearance of two distinct cycle lengths in gypsy moth defoliation data may result from the aggregation of data across heterogeneous locations (Johnson et al. 2006b; Haynes et al. 2009b). The dominant outbreak cycle length differs between different forest types, possibly due to the abundance of preferred hosts (Johnson et al. 2006b) or predator densities (Bjørnstad et al. 2010). Though variation in these environmental conditions is continuous, Bjørnstad et al. (2010) demonstrated that dispersal between two model populations allowed only for the discrete, subharmonic cycle lengths seen in the defoliation data. However, oscillations at both cycle lengths are present at small spatial scales (Haynes et al. 2009b), indicating that this phenomenon may be generated within a single population. Gypsy moths interact with a wide variety of hosts, pathogens, parasitoids, and predators that are not included in our population model (Elkinton and Liebhold 1990) and may contribute to more complex population dynamics.

In this study, we examined an 86-year gypsy moth time series and found that population behavior was temporally quite variable, demonstrating multiple shifts between cyclical and noncyclical behavior during the study period. The collapse of previously stable population cycles in other species have frequently been linked to long-term alterations to the environment, such as climate change (Ims et al. 2008 and references therein). In contrast, our results suggest that the trophic interactions thought to govern gypsy moth populations can produce variable population behavior, even in the absence of drastic environmental changes.

Complex ecological interactions can make it difficult to identify mechanisms causing changes in population behavior (Ims et al. 2008), and this study highlights the extensive knowledge of a species' ecology and the long time series required to draw definitive conclusions.

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