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ORIGINAL ARTICLE

Elevational gradient in the cyclicity of a forest-defoliating insect

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Abstract Observed changes in the cyclicity of herbivore populations along latitudinal gradients and the hypothesis that shifts in the importance of generalist versus specialist predators explain such gradients has long been a matter of intense interest. In contrast, elevational gradients in population cyclicity are largely unexplored. We quantified the cyclicity of gypsy moth populations along an elevational gradient by applying wavelet analysis to spatially referenced 31-year records (1975–2005) of defoliation. Based on geographically weighted regression and nonlinear regression, we found either a hump-shaped or plateauing relationship between elevation and the cyclicity of gypsy moth populations and a positive relationship between cyclicity and the density of the gypsy moth's preferred host-tree species. The potential effects of elevational gradients in the density of generalist predators and preferred host-tree species on the cyclicity of gypsy moth populations were evaluated with mechanistic simulation models. The models suggested that an elevational gradient in the densities of preferred host tree species could partially explain elevational patterns of gypsy moth cyclicity. Results from a model assuming a type-III functional response of generalist predators to changes in gypsy moth density were inconsistent with the observed elevational gradient in gypsy moth cyclicity. However, a model with a more realistic type-II functional response gave results roughly consistent with the empirical findings. In contrast to classical studies on the effects of generalist predators on prey population cycles, our model with a type-II functional response predicts a unimodal relationship between generalist-predator density and the cyclicity of gypsy moth populations.

Keywords Gypsy moth · *Lymantria dispar* · *Peromyscus leucopus* · Population cycle · Periodicity

Introduction

For many decades, ecologists have pondered why some animal populations exhibit multi-annual cycles in abundance. The study of population cycles has helped answer some of the most vexing questions in population ecology, such as how coexistence is maintained in predator–prey systems and the relative importance of intrinsic (e.g., trophic dynamics) versus extrinsic (e.g., weather) drivers (Elton 1924; Moran 1949; Keith et al. 1984; Coulson et al. 2004). The study of geographic gradients in the degree of cyclicity of oscillations in abundance has proven valuable in this regard. A number of vertebrate species (e.g., voles, lemmings, grouse, snowshoe hares) and a forest insect, the autumnal moth, are known to exhibit greater cyclicity at higher latitudes (e.g., Wolff 1980; Bjørnstad et al. 1995; Klemola et al. 2002; but see Kendal et al. 1998). In several

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cases (reviewed in Lambin et al. 2006), researchers have suggested that latitudinal gradients in the relative importance of generalist compared to specialist predators underlie this pattern. Destabilization of prey population dynamics at high latitudes has been attributed to relatively weak influence of generalist predators (Hansson 1987; Hanski et al. 1991). Cycles are an intrinsic result of tight coupling of predator and prey populations, such as when the main predator is a specialist and generalist predators are relatively less important. Given reports that faunal species diversity declines with increasing elevation (Rahbek 1995; Gaston and Williams 1996; Brown 2001; Sergio and Pedrini 2007), we might expect to find declining influence of generalist predators with increasing elevation, whereas specialist predators might persist wherever their prey is present. Consequently, herbivore populations may tend to become more cyclical with increasing elevation. However, elevational gradients in cyclicity are largely unexplored.

Generalist predators are usually expected to exhibit type-III functional responses to changes in the density of their prey (Holling 1965; Hanski et al. 1991; Schenk and Bacher 2002), meaning that the feeding rate per predator is expected to increase in an accelerating fashion as the density of prey increases. The type-III functional response of the generalist predators is a key component of past theoretical studies examining the role of specialist versus generalist predators in driving latitudinal gradients in cyclicity (e.g., Hanski et al. 1991; Turchin and Hanski 1997). In some cases, however, feeding efficiency (or preference for a prey species) of generalists may decline with increasing density of the prey, as in a type-II functional response. For example, Elkinton et al. (1989, 1996) conclude that the generalist mammalian predators of gypsy moths (*Lymantria dispar* L.) collectively exhibit a type-II functional response to changes in gypsy moth density.

Elevation is an important factor influencing the abundance and foraging habits of the small mammalian generalists preying on gypsy moths. Densities of these generalists are typically lower in higher-elevation sites likely because shrub and herbaceous layers are not well developed on xeric slopes and ridgetops (Campbell 1981; Smith 1983, 1985; Yahner and Smith 1991; Brooks et al. 1998). For example, in a 16-year survey of small mammals in Vermont, USA, recaptures of small mammals [chiefly *Peromyscus leucopus* Rafinesque (white-footed mouse), *Myodes gapperi* Vigors (southern red-backed vole), and various shrews] were 12.1 and 14.5% higher at low- than at mid- and high-elevation sites, respectively (Brooks et al. 1998). In addition, because alternative food sources (e.g., fruit produced by *Vaccinium* spp.) are more available at high elevations, some key generalist predators (e.g., *Peromyscus leucopus*) feed less intensively on gypsy moths at high elevations (Smith 1989).

Tree species composition in the northeastern United States also varies considerably with elevation; ridge-top stands often consist of xerophilic mixtures of *Quercus* and *Pinus* spp. whereas stands at lower elevations often are dominated by *Quercus* mixed with *Acer* and other mesophytic species (Houston and Valentine 1977). Gypsy moth larvae are highly polyphagous, feeding on >200 tree species in North America, but larvae display strong preferences for certain species (Liebhold et al. 1995). Though larvae will feed on less preferred hosts, their survivorship and fecundity are generally higher when feeding on preferred tree species (Hamilton and Lechowicz 1991).

The frequency of gypsy moth outbreaks is known to increase with increasing elevation (Bess et al. 1947; Houston and Valentine 1977; Liebhold et al. 1994). However, no studies have evaluated whether the cyclicity of gypsy moth outbreaks varies across elevations. In this paper, we explored whether the cyclicity of gypsy moth outbreaks changes with elevation by applying wavelet analysis to a 31-year record of forest defoliation in the northeastern United States. We evaluated whether elevational changes in the cyclicity of gypsy moth outbreaks may be caused by elevational gradients in the density of generalist predators or the density of the gypsy moth's preferred host trees. To explore how the cyclicity of gypsy moth outbreaks may be affected by elevational differences in predation pressure or density of preferred host trees, we used mechanistic simulation models of multitrophic interactions between gypsy moths, generalist predators, and a specialist viral pathogen of the gypsy moth. We compared the predictions of models with both type-III and type-II functional responses by generalist predators to changes in gypsy moth density.

Methods

Study system

The gypsy moth, although native to Eurasia, has invaded over 1 million km^2 of forest in North America (Liebhold et al. 1992). Populations of the gypsy moth usually occur at such low densities that the species is virtually undetectable, but occasionally densities grow rapidly to outbreak levels (Liebhold et al. 2000). In northeastern North America, outbreaks exhibit two significant periodicities; outbreaks occur with dominant periods of 4–5 and 8–10 years (Johnson et al. 2006; Haynes et al. 2009). Because outbreaks are partially synchronized over ca. 1000 km (Peltonen et al. 2002), outbreaks lead to simultaneous defoliation of large areas of forest (Liebhold et al. 2000). Outbreaks of forest defoliating insects such as the gypsy moth can have major adverse impacts on tree survival, forest productivity, and nutrient cycling (Davidson et al. 2001; Christenson et al. 2002).

Although small mammals (e.g., *Peromyscus* and shrews) are the main predators of the gypsy moth, these generalist predators do not respond numerically to gypsy moth abundance and only cause high rates of mortality when gypsy moth densities are low (Elkinton and Liebhold 1990; Elkinton et al. 1996). During the low-density phase of the gypsy moth's population cycle, sufficiently dense predator populations inhibit gypsy moth population growth. However, when gypsy moth density increases and the moth largely escapes the effect of predators, the largest source of mortality for the gypsy moth is typically disease, either caused by the gypsy moth nucleopolyhedrosis virus (NPV; Elkinton and Liebhold 1990) or by the entomopathogenic fungus *Entomaphaga maimaiga* (Hajek et al. 1995).

Geographically referenced outbreak data

The cyclicity of gypsy moth outbreaks was assessed by analyzing an archive of defoliation survey maps covering the northeastern United States over a period of 31 years (1975–2005). These maps were digitized and represented as sequential raster layers in a geographic information system (GIS). Individual quadrats (rasters) were 2 × 2 km. Analyses here were restricted to regions designated as part of the 1975 generally infested area in US Dept. of Agriculture gypsy moth quarantine regulations (US Code of Federal Regulations, Title 7, Chapter III, Sect. 301.45). Data from areas more recently infested by the gypsy moth were not included in our analysis because of the short history of defoliation in these areas. We also excluded any quadrats in which defoliation was detected <3 years because these quadrats do not provide useful information about cyclicity.

Given the presence of steep, mountainous terrain within the gypsy moth's range in North America, analyzing the defoliation data at the finest available resolution (2 × 2 km) may appear the most sensible approach to characterizing elevational gradients in the cyclicity of gypsy moth outbreaks. However, analysis of outbreak cyclicity using fine-resolution, aerial-survey data tends to be plagued by spatial errors (Bjørnstad et al. 2010). Yearly defoliation surveys are conducted by airborne observers sketching defoliated areas onto maps, a process which involves some degree of error (Ciesla 2000). Ultimately, individual map rasters are scored as defoliated (1) or not defoliated (0). As a result of spatial error and binary coding, the defoliation data for individual 2 × 2 km rasters has high rates of errors of omission or commission (Bjørnstad et al. 2010). In addition, important spatiotemporal patterns of population dynamics may be apparent only at broad spatial scales owing to high local variability in environmental conditions (Liebhold et al. 2000; Bjørnstad et al. 2010). Given our conflicting needs to account for the effects of fine-scale variation in elevation while minimizing spatial error and stochastic variation in gypsy moth defoliation, our approach was to conduct 2-dimensional smoothing of the 2 × 2 km resolution annual defoliation data. The data were smoothed using a two-dimensional cubic spline (known as a thin-plate spline; smoothing parameter $= 5 \times 10^{-5}$; Hutchinson and Gessler 1994).

Wavelet analysis was then performed on the spatially smoothed defoliation time series for each 2 × 2 km quadrat to evaluate changes in the strength of defoliation cyclicity (measured as wavelet power; Torrence and Compo 1998; Liu et al. 2007) across the elevational gradient. Wavelet analysis is similar to Fourier analysis in that both are used to extract frequency information from a signal, but differs in that wavelet analysis can be applied to time series where the frequency and amplitude of oscillations vary through time (Torrence and Compo 1998). Wavelet analysis determines how well wavelets (oscillating periodic functions) approximate a time series (Torrence and Compo 1998). The wavelet transform, the measure of correspondence between a wavelet function and the time series data, is computed as the integral of the amount of overlap as the wavelet function is slid across the time series. The dominance of signals of different period length in the time series data is determined by comparing the power (square of the wavelet transforms) of wavelets of varying scale (width), using a known relationship between scale and period length (Torrence and Compo 1998). We used the Morlet wavelet function, a modified sine wave that is localized in time by damping it with a Gaussian envelope (Farge 1992; Grenfell et al. 2001). Prior to performing wavelet analysis, the time series were square-root transformed (after adding 1.16 to each observation to eliminate negative values) to normalize the distributions of observations (Sardeshmukh et al. 2000). Furthermore, the time series were standardized to have means of zero and standard deviations of one (Torrence and Compo 1998).

Liu et al. (2007) demonstrated that the traditional method of computing power spectra from wavelet analysis is biased towards producing higher power values for low-frequency (long period) signals. Because the range of integration increases with wavelet scale, power integrated across time tends to be greater at larger scales (Liu et al. 2007). To correct for this bias, we follow the protocol recommended by Liu et al. (2007), which is to divide the wavelet power by the wavelet scale.

We evaluated the relationships between elevation, density of preferred host trees, and the strength of cyclicity (wavelet power at the spectral peak) in gypsy moth defoliation. Power at the spectral peak was used to assess the degree of cyclicity in each defoliation time series because this value indicates the amount of variance explained at the dominant frequency. Relationships between elevation, density of preferred host trees, and cyclicity were evaluated by performing ordinary least-squares regression (global) and geographically weighted regression (GWR; Fotheringham et al. 2002) using the GWR 3.0 software package. These two regression approaches provide complementary information about relationships between environmental variables and dependent variables across space. OLSR models provide a single, global estimate of the regression parameter for each environmental variable; however, they cannot account for spatial autocorrelation or nonstationarity (spatial heterogeneity in the relationships between predictor and dependent variables across space; Fotheringham et al. 2002). The GWR approach does not provide such global parameter estimates, yet spatial dependence and nonstationarity are modeled explicitly by fitting a series of local regressions. A local regression model is generated for each sampled location by using data from the focal location as well as data from nearby locations with each data point j inversely weighted by its distance d_{ij} from the focal location i. Because a local model is generated for each location, nonstationarity does not interfere with fitting the relationships between environmental and dependent variables. GWR addresses the problem of spatially autocorrelated residuals by absorbing spatially varying relationships in the parameter estimates, not the error term as is done in any type of global regression (Fotheringham et al. 2002).

The data for each local regression were weighted using a bi-square weight function,

$$\begin{aligned} g_i &= \left(1 - \left(d_{ij}^2\right)/b^2\right)^2 \quad \text{if} \quad d_{ij} < b, \\ &= 0 \quad \text{if} \quad d_{ij} > b, \end{aligned} \tag{1}$$

which is approximately Gaussian for distances $<b$ and zero for distances $>b$ (Brundson et al. 1996; Fotheringham et al. 2002). The distance at which the weights decline to zero, b, was allowed to adapt to the availability of data (i.e., longer distances in parts of the gypsy moth's range with a low density of 2 × 2 km quadrats) to avoid scarcities of data. Adaptive fitting of the weight kernels was achieved through cross validation, a procedure in which the optimal value of b is the value that minimizes the score function

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

where $\hat{y}_{\neq i}$ represents the predicted value of y_i, the wavelet power observed at location i, with the data from location i omitted from the calculation (Fotheringham et al. 2002).

An information-theoretic approach (Burnham and Anderson 2002) was used to select among a set of candidate GWR models to determine which model provided the most parsimonious fit to the data. In this approach, candidate models containing different predictor variables are ranked based on fit balanced by a penalty for increasing numbers of predictor variables through computation of AIC values. The relative support for each model was evaluated with AIC differences (ΔAIC_i), $\Delta\text{AIC}_i = (\text{AIC})_i - \text{minAIC}$, where minAIC is the AIC of the best-fitting model. For model i, the plausibility that it is the best model decreases with increasing ΔAIC_i. Models with values $\Delta\text{AIC}_i < 2$ were considered to have substantial support (Burnham and Anderson 2002). In addition, we computed the approximate probability that a model within the set of R models was the best model by calculating its Akaike weight (w_i):

$$w_i = \frac{\exp\left(-\frac{\Delta\text{AIC}_i}{2}\right)}{\sum_{r=1}^{R} \exp\left(-\frac{\Delta\text{AIC}_r}{2}\right)}. \tag{3}$$

Because preliminary plots appeared to indicate a hump-shaped or plateauing relationship between elevation and maximum wavelet power, we compared the fits of linear and quadratic models in GWR. To evaluate the possibility of a plateauing relationship between elevation and power, we performed non-spatial nonlinear regression since nonlinear fitting procedures have not been developed for GWR. The plateauing function was specified as log(maximum power) $= p_0 + (p_1 \times \text{elevation})/(\text{elevation} + p_2)$, where p_0 is the intercept, p_1 is the asymptote, and p_2 determines the curvature. The fit of this plateauing function was compared to the fit of a non-spatial quadratic model. In this case, the fits of these models were compared based on R^2 values since the models contained equal numbers of parameters. Prior to all regression analyses, maximum wavelet power was *log* transformed to minimize heterogeneity of variance.

Elevation data were obtained from US Geological Survey 1:250000 Digital Elevation Models (Elassal and Caruso 1983). Host-tree density was obtained from a 1 km raster GIS layer developed by Morin et al. (2005). To develop this raster layer, host basal area was interpolated across >90000 forest inventory plots (Kingsley 1985). Host basal area was then adjusted for forest density by multiplying interpolated host basal area by percentage forest cover (Morin et al. 2005). Eastern North America contains 79 species 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 host-tree density data used here consisted of the sum of the basal area per ha across all preferred hosts.

Multitrophic model

We examined the consequences of variation in densities of generalist predators and preferred host trees across elevational gradients based on a model first developed by Dwyer et al. (2004) and modifications made by Bjørnstad et al. (2010). Dwyer et al.'s (2004) model was developed based on extensive study of virus transmission in field and laboratory experiments (Dwyer and Elkinton 1993; Dwyer et al. 1997) as well as experimental data on the gypsy moth's interactions with small-mammal predators (Elkinton et al. 1996). One of Bjørnstad et al.'s (2010) main modifications was to model the effects of NPV and predators sequentially. In accordance with the timing of these mortality sources in field populations, viral infection was imposed during the larval stage and predation during the pupal stage. The density of larvae in year t can be calculated as

$$\tilde{N}_t = \lambda N_{t-1} \tag{4}$$

where λ is the mean number of female larvae produced per adult female and N_{t-1} is the density of adult females in year $t-1$. The fraction of these larvae that are infected and ultimately killed by NPV, $I(\tilde{N}_t, \tilde{Z}_t)$, is dependent on the densities of larvae $(\tilde{N}_t)$ and viruses $(\tilde{Z}_t)$, respectively. Dwyer et al. (2000, 2004) derived an implicit function for computing the fraction killed by NPV given by

$$1 - I(\tilde{N}_t, \tilde{Z}_t) = \left(1 + \frac{\bar{v}}{\mu k}\left(\tilde{N}_t I(\tilde{N}_t, \tilde{Z}_t) + \rho \tilde{Z}_t\right)\right)^{-k}, \tag{5}$$

where μ is the rate at which cadavers lose infectiousness, ρ is the susceptibility of hatchlings relative to later-stage larvae, $\bar{v}$ is the average transmission rate, and k is the inverse squared coefficient of variation of transmission rate. The density of individuals escaping infection and surviving to the pupal stage is then

$$N'_t = \tilde{N}_t\left(1 - I(\tilde{N}_t, \tilde{Z}_t)\right). \tag{6}$$

Moreover, viral density in generation $t+1$ can be calculated as

$$Z_{t+1} = f \tilde{N}_t I(\tilde{N}_t, \tilde{Z}_t), \tag{7}$$

where f is the over-winter growth rate of the pathogen.

During the pupal stage, predation by small mammals is the largest cause of mortality in low density gypsy moth populations (Elkinton and Liebhold 1990; Elkinton et al. 1996). Results from experimental studies differ as to whether predation of gypsy moth pupae becomes more or less intense as pupal density increases from low to moderate levels (Elkinton et al. 2004; Schauber et al. 2004). Therefore, in this study, we compare predictions from a model assuming a type-III functional response of the predator to a model assuming a type-II response. Modifying Dwyer et al.'s (2004) type-III model to account for stage structure and variable predator densities, we compute the instantaneous predation rates on pupae in year t as $abP_t N'_t / \left(N'^2_t + b^2\right)$ where a determines (but does not equal) the maximum number of prey individuals killed per predator and b is the pupal density for which predation rate is maximized. Assuming a Poisson distribution for the probabilities of encounter between predators and prey, the per-capita probability of not being killed by predators is modeled as $\exp\left[-abP_t N'_t / \left(N'^2_t + b^2\right)\right]$ (Rogers 1972). Our model of adult gypsy moth dynamics based on a type-III functional response, and including stochastic variation in population growth (e^{v_t}), is then

$$N_t = N'_t \exp\left(-\frac{abP_t N'_t}{N'^2_t + b^2}\right) e^{v_t}. \tag{8}$$

We can model a type-II functional response by computing the instantaneous rate of predation in year t as $cdP / \left(N'_t + d\right)$, where c determines the maximum fraction of prey killed and d determines the half-saturation point (the density at which the number of prey killed is half of the maximum killed). Our model of adult gypsy moth dynamics using a type-II functional response is then

$$N_t = N'_t \exp\left(-\frac{cdP_t}{N'_t + d}\right) e^{v_t}. \tag{9}$$

We incorporate stochastic variation in population growth into Eqs. 8 and 9 because the density of adult females determines the initial number of larvae in the following generation. Here, v_t is a normally distributed random variable with a mean of zero. The variance of v_t was set at 1 in both the type-III and type-II model. This level of stochasticity caused density to fluctuate across 4 orders of magnitude in the type-III model, as was observed in field populations of the gypsy moth (Berryman 1991). In the type-II model, the magnitude of fluctuations in gypsy moth density was relatively insensitive to the level of stochasticity. In Eqs. 8 and 9, we used values for a (=7.82), b (=0.05), c (=3.91), and d (=0.017) that provided similar characteristics to the empirically derived type-III functional response of Dwyer et al. (2004) [Appendix S1 in Electronic Supplementary Material (ESM)].

Two model parameters (P and λ) were varied to simulate the effects of elevational gradients in predation pressure and density of preferred tree species. An elevational gradient in predation pressure was simulated by varying the density of the generalist predator (P). We selected a maximum predator density (P) such that simulated predator populations were sufficiently dense to strongly reduce the frequency of gypsy moth outbreaks, but did not eliminate outbreaks altogether. For both the type-III and type-II model, predator density was incrementally varied between 0.01 and 1. We simulated the effect of elevational changes in the density of preferred tree species by varying gypsy moth fecundity (λ), based on experiments demonstrating that gypsy moths fed on preferred tree species have higher fecundity (Hamilton and Lechowicz 1991). The range of fecundity values used was ±50% of the empirical estimate (Dwyer et al. 2004) of 74.6. The values for the additional parameters in Eqs. 4, 5, and 7 dealing with host-viral dynamics were derived from field and laboratory experiments and observations of the dynamics of field populations (Elkinton et al. 1996; Dwyer et al. 2004; $\bar{\nu} = 0.9$, $\mu = 0.32$, $k = 1.06$, $\rho = 0.8$, and $f = 21.33$). We set a minimum viral density of 0.0001. This minimum functioned to prevent extinctions of NPV and may mimic rescue effects due to dispersal (Schauber 2001).

Population fluctuations were simulated over 550 years. Initial gypsy moth and virus densities were drawn from random, normal distributions. To reduce the influence of transient dynamics resulting from initial conditions, the first 50 years of data from each time series were discarded prior to statistical analysis of the time series. For each of the resulting time series, we examined the strength of cyclicity of gypsy moth population fluctuations using wavelet analysis (Torrence and Compo 1998; Liu et al. 2007).

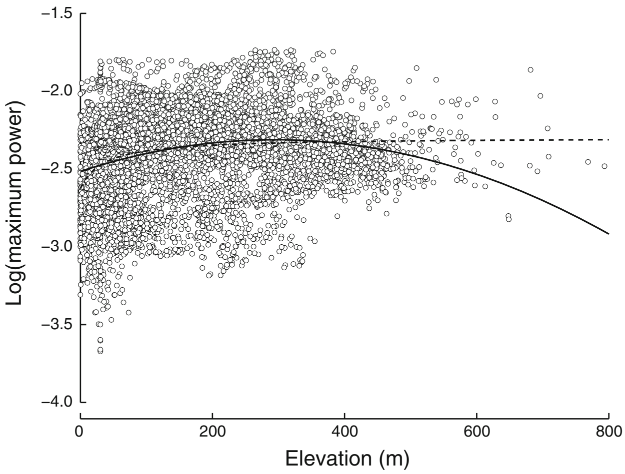


Fig. 1 Global elevational gradient in cyclicity of defoliation (maximum wavelet power). The fitted relationship from a quadratic function [log(maximum power) = $1.36 \times 10^{-3} \times$ elevation − $2.31 \times 10^{-6} \times$ elevation^2 − 2.51, $n = 7084$, $R^2 = 0.06$] is displayed with a *solid line*. The fitted relationship for a plateau function [log(maximum power) = 0.33 × elevation/(elevation + 32.32) − 2.63, $n = 7084$, $R^2 = 0.06$] is displayed with a *dashed line*

Results

Outbreak data

Using non-spatial (global) OLSR models, we could not determine if the cyclicity of gypsy moth defoliation (measured as maximum wavelet power) was highest at mid or upper elevations. The variances explained by fitting quadratic and plateauing functions to the relationship between elevation and cyclicity were low and nearly identical (both with $R^2 = 0.06$; Fig. 1).

In contrast, the GWR models we considered (which account for nonstationarity and spatial autocorrelation) explained up to 76.8% of the variation in the strength of cyclicity. A GWR model with elevation, elevation^2, and host density as predictor variables received the greatest level of support (Table 1). This model received substantially more support than the model with only elevation and host density (ΔAIC = 158.45). The full model also received substantially more support than the model with elevation alone (ΔAIC = 559.36) or the model with host density alone (ΔAIC = 917.48). The approximate probability that the GWR model with all three predictor variables was the best model was >0.99 (based on w_i). Mean global wavelet power spectra of the defoliation data within five elevation classes are displayed in Appendix S2 in ESM.

Density of the gypsy moth's host trees tended to be highest at mid elevation, evidenced by the fact that a GWR model with the predictor variables elevation and elevation^2 received greater support than a model with elevation alone (based on comparison of AIC values; ΔAIC = 225.13). This quadratic GWR model explained 64.76% of the variation in host-tree density. The variation explained by fitting a non-spatial (global) OLSR model with a quadratic relationship between elevation and host-tree density was

Table 1 Ranking of linear and quadratic geographically weighted regression models for predicting the strength of cyclicity in the defoliation time series based on elevation and host-tree density

Model rank	Model	AIC	ΔAIC	Akaike weights	R^2
1	Host × elevation × elevation^2	−8792.66	0	>0.99	0.77
2	Host × elevation	−8634.23	158.45	3.92×10^{-35}	0.76
3	Elevation	−8233.30	559.36	3.40×10^{-122}	0.74
4	Host	−7875.19	917.48	5.90×10^{-200}	0.73

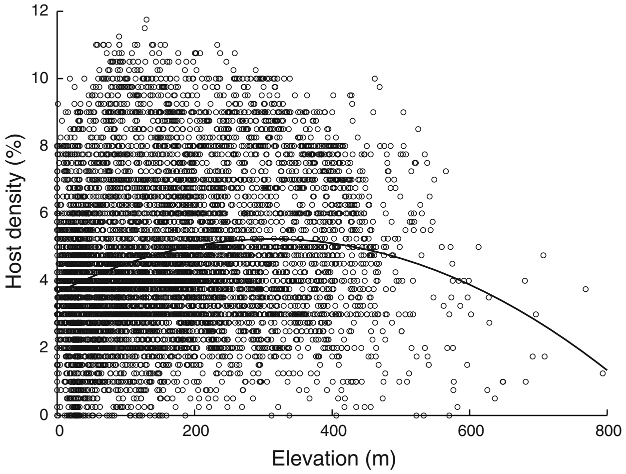


Fig. 2 Elevational gradient in the density of the gypsy moth's preferred host trees (percent of forest area). The global relationship is shown here by regressing host density against elevation and elevation^2 (host density = 0.01 × elevation − 1.63 × 10^{-5} × elevation^2 + 3.64, $n = 7084$, $R^2 = 0.05$)

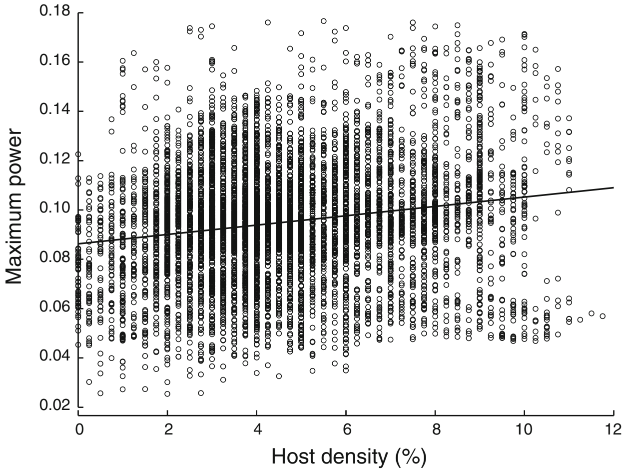


Fig. 3 Relationship between cyclicity of defoliation (maximum wavelet power) and host density. The global relationship is shown here by regressing maximum power against host density (maximum power = 1.86 × 10^{-3} × host density + 0.09, $n = 7084$, $R^2 = 0.03$)

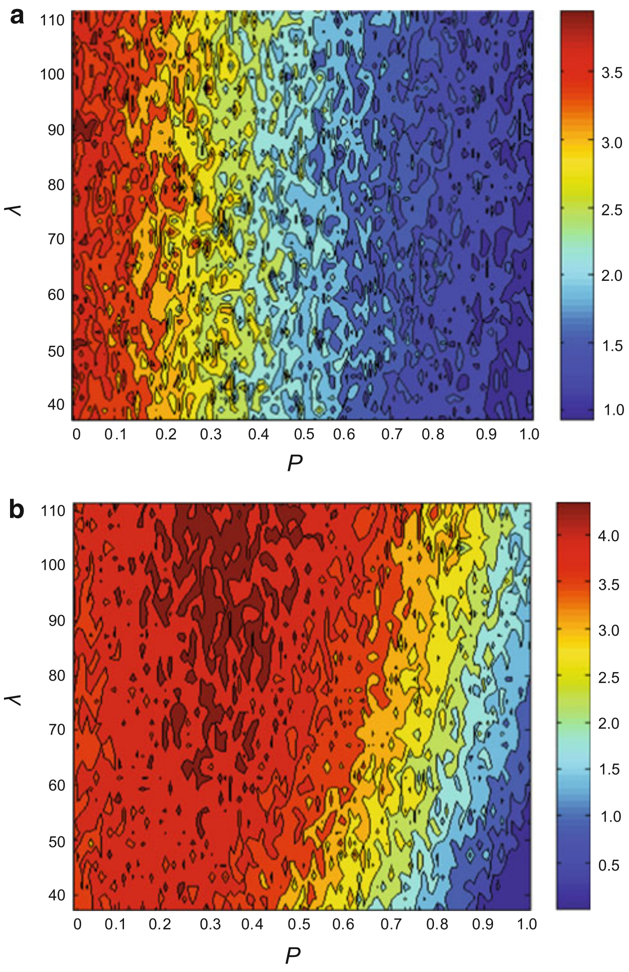


Fig. 4 Contour plots showing the strength of cyclicity (maximum wavelet power) of simulated gypsy moth populations in relation to density of the generalist predator (P) and gypsy moth fecundity (λ). Predator was modeled with a type-III functional response (**a**) and a type-II functional response (**b**) to changes in gypsy moth density

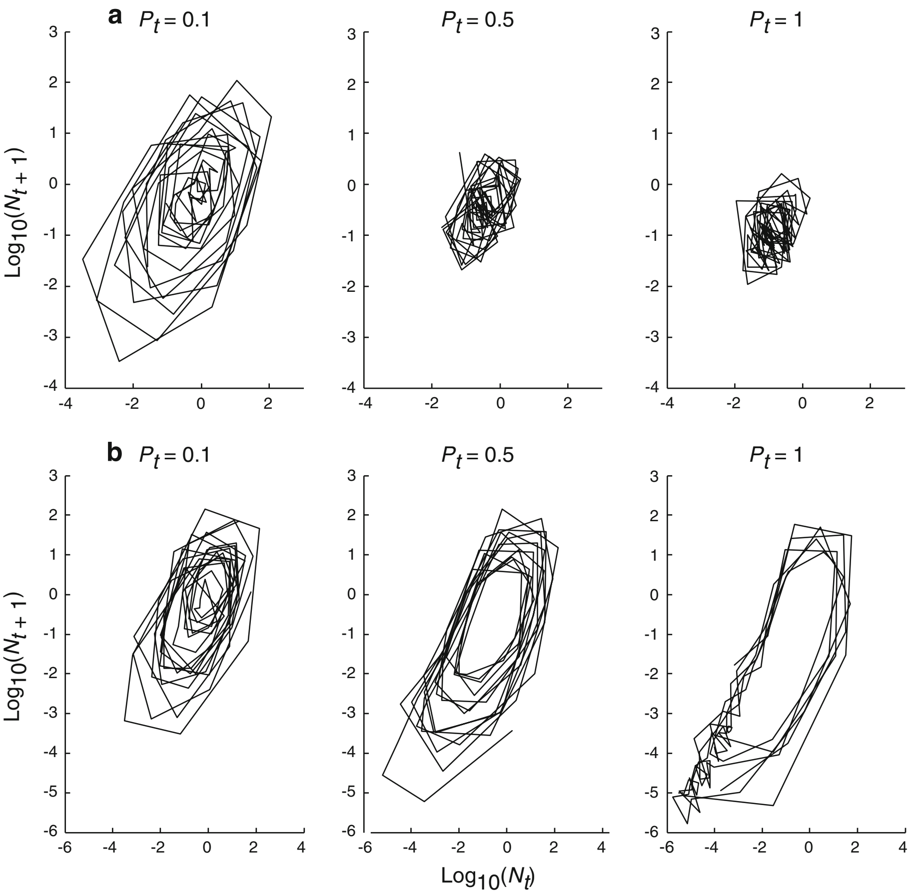
much lower (Fig. 2). The cyclicity of gypsy moth defoliation increased monotonically with host density (Fig. 3).

Multitrophic model

Using a type-III functional response by the generalist predator, the cyclicity of simulated gypsy moth populations generally decreased with increasing predator density and was unaffected by gypsy moth fecundity (Fig. 4a). In contrast, when a type-II functional response was used, cyclicity of gypsy moth populations was highest at intermediate predator densities (Fig. 4b). Furthermore, cyclicity generally increased with fecundity (Fig. 4b).

Phase portraits from the model using a type-III functional response show that oscillations of gypsy moth density became increasingly compact as predator density was increased (Fig. 5a). Using a type-II functional response, the amplitude of oscillations increased with increasing predator density (Fig. 5b). Populations crashed to much lower densities and the depth of the crash increased greatly with increasing predator density. The trajectory of the gypsy moth population with intermediate predator density was more regular than at low predator density. At high predator density, gypsy moth population trajectories were irregular when gypsy moth density was low, with high variability in the number of time steps before the population recovered to moderate densities (Fig. 5b).

Fig. 5 Phase portrait of the simulated gypsy moth populations at low, intermediate, and high predator densities. Predator was modeled with a type-III functional response (**a**) and a type-II functional response (**b**) to changes in gypsy moth density. For all phase portraits, $\lambda = 74.6$ (Dwyer et al. 2004)



Discussion

Given the lack of research on population cycles along elevational gradients, perhaps the best parallel to our study is the significant body of work on latitudinal gradients in population cycles (e.g., Wolff 1980; Bjørnstad et al. 1995; Kendal et al. 1998; Cattadori and Hudson 1999; Johnson et al. 2000; Murray 2000; Klemola et al. 2002). Among the potential mechanistic explanations for observations of stronger cycles at high latitudes, the hypothesis that has received the greatest level of support is that this is due to greater densities or effectiveness of generalist predators at low latitudes (Hansson 1987; Hanski et al. 1991; Bjørnstad et al. 1995). Using a model including both specialist and generalist natural enemies of a common prey species, Hanski et al. (1991) showed that direct density dependence imposed on the prey by generalist predators with a type-III functional response can inhibit predator–prey cycles that would otherwise develop due to the delayed-density-dependent mortality caused by specialist natural enemies. There is considerable empirical evidence in our system that densities of generalist predators are higher at lower elevations (Campbell 1981; Smith 1983, 1985; Yahner and Smith 1991; Brooks et al. 1998), yet we did not find a simple positive relationship between elevation and the strength of cyclicity in gypsy moth outbreaks. From low to intermediate elevation, outbreak cyclicity increased with increasing elevation. However, outbreak cyclicity declined or plateaued with increasing elevation from mid to upper elevation (Fig. 1). This relationship between elevation and the cyclicity of gypsy moth outbreaks may be partially attributed to elevational differences in the density of the gypsy moth's preferred host trees (Fig. 2). The susceptibility of forests to defoliation by the gypsy moth is largely a function of the density of the moth's preferred host trees; defoliation frequency increases with increasing dominance of preferred host species (e.g., oaks; Liebhold et al. 1997). The best GWR model contained host-tree density as a predictor variable, but it also included the predictor variables elevation and elevation^2. Because the GWR models were ranked based upon AIC values, a measure of fit that penalizes for increasing numbers of parameters (Burnham and Anderson 2002), the model rankings suggest that the elevational gradient in the density of preferred host trees alone does not fully explain the relationship between elevation and the cyclicity of gypsy moth outbreaks.

Our simulation-model results suggest an explanation for the empirical elevation-cyclicity relationship. When generalist predators exhibited a type-II functional response (but not a type-III functional response), the model predicted a hump-shaped relationship between predator density and the cyclicity of gypsy moth populations (Fig. 4b) similar to the relationship between elevation and cyclicity observed in historical data (Fig. 1). Populations of generalist predators do not exhibit a numerical response to gypsy moth densities in the model, which is consistent with the behavior of generalist predators in this system (Elkinton and Liebhold 1990). Under this condition, the type of functional response is important mainly when gypsy moth density is low, i.e., following a population crash. Classical studies on the effects of generalist predators on prey cycles predict that a generalist predator exhibiting a type-III functional response would exert stabilizing negative density dependence across a moderate range of prey densities (Murdoch and Oaten 1975; Hanski et al. 1991; Turchin and Hanski 1997). This likely explains why our model with a type-III functional response predicted declining cyclicity of the gypsy moth with increasing predator density. In contrast, a type-II functional response by the predator is not stabilizing and produces an Allee effect (Bjørnstad et al. 2010). In our simulations, we found that this Allee effect caused gypsy moth populations to crash to lower levels than they would under a type-III functional response. When the density of the type-II predator was set to an intermediate level, the increased depth of the gypsy moth population crash strengthened the host-pathogen oscillations, producing a well-defined orbit through phase space (Fig. 5b). Predation resulting in a weak Allee effect can enhance host-pathogen oscillations in this system because deeper and longer gypsy moth population crashes lead to sharp periodic declines in pathogen-induced mortality (Bjørnstad et al. 2010). However, above intermediate predator densities, we found that a predator exhibiting a type-II functional response could cause gypsy moth density to remain extremely low for long periods of time and reduce cyclicity in host-pathogen oscillations. Given these findings, the elevational gradient in generalist predator (small mammal) density (Campbell 1981; Smith 1983, 1985; Yahner and Smith 1991; Brooks et al. 1998) and the rate at which they feed on gypsy moth pupae (i.e., lower rate of feeding at high elevation; Smith 1989) could underlie the elevational patterns of cyclicity displayed by gypsy moth populations.

Most empirical studies of small-mammal predation on gypsy moths indicate the proportion of prey consumed declined with increasing prey density as with a type-II functional response (Elkinton et al. 1989, 1996; Grushecky et al. 1998, but see Schauber et al. 2004). Elkinton et al. (2004) found that gypsy moth pupae are low in palatability relative to alternative food sources. As a result, predators likely do not switch to selectively feeding on gypsy moths in response to increased gypsy moth density, in which case a type-II functional response is expected (Holling 1959; Murdoch 1973). Furthermore, there is considerable empirical and theoretical evidence that low-density gypsy moth populations are subject to Allee effects, which may be due to both mate-finding failure and predation (Liebhold and Bascompte 2003; Whitmire and Tobin 2006; Tobin et al. 2007; Bjørnstad et al. 2010).

In addition to elevational changes in generalist predator density, a hump-shaped relationship between gypsy moth fecundity and elevation could explain the empirical elevation-cyclicity relationship. A hump-shaped relationship between fecundity and elevation is plausible given that host tree density is highest at intermediate elevations (Fig. 2) and that gypsy moth fecundity is highest when feeding on preferred tree species (Hamilton and Lechowicz 1991). Higher rates of population growth may increase the magnitude of outbreaks and hasten population crashes (resulting from density-dependent mortality; Elkinton and Liebhold 1990; Dwyer et al. 2004), leading to strong oscillations in gypsy moth density. Previous studies have revealed that defoliation frequency (Liebhold et al. 1994) and the dominant period length of gypsy moth cycles differ among forest types (Johnson et al. 2006); however, the observed positive relationship between gypsy moth outbreak cyclicity and the density of preferred host trees is a novel finding of this study.

Although we have focused on distributions of host-tree species and natural-enemy-mediated effects of elevation on gypsy moth population dynamics, elevation may affect gypsy moths through other mechanisms as well. Temperature differences across elevations, for example, might be expected to cause variation in synchrony between larval hatching and budburst of host trees. Whereas the timing of gypsy moth hatching is known to be driven primarily by winter and spring temperatures (Gray et al. 2001), the timing of budburst in trees is often influenced not only by temperature, but also photoperiod (Körner and Basler 2010), which is not related to elevation. As a result, it is possible that an elevation-temperature cline could decouple the timing of gypsy moth hatching from budburst. However, Hunter and Elkinton (2000) experimentally studied the consequences of such decoupling and found that effects of the timing of budburst and natural enemy induced mortality were opposing; thus, these effects may tend to cancel each other out and the overall impact of seasonal decoupling may be minimal in this system.

Another factor that could differentially affect gypsy moth population dynamics at low versus high elevation is the nutritional quality of foliage; Erelli et al. (1998) found that leaf nitrogen levels in several tree species were greater at high than low elevation sites. In addition, leaf tannin levels were lower at high elevation. The increased nutritional quality of leaves at high elevation was shown to have several positive effects on gypsy moths (increased survival, shortened development time, increased fecundity) that might affect population dynamics. For example, low-quality forage at low elevations could intensify direct density dependence associated with intraspecific competition for food. An increase in the strength of direct density dependence caused by poor leaf quality would be expected to cause a decay of cyclicity (Royama 1992; Ims et al. 2008). However, under this mechanism we would expect a positive relationship between elevation and the cyclicity of gypsy moth populations rather than the observed hump-shaped or plateauing relationship.

Our findings complement the body of literature underscoring macroecological patterns in population cyclicity, but more notably our findings document a novel elevational gradient in population cyclicity. The relationship between elevation and cyclicity of gypsy moth populations may result from the elevational gradients in generalist predator densities, preferred host trees, or a combination of both. Furthermore, in stark contrast with classical studies on the effects of generalist predators on population cycles (Hansson 1987; Hanski et al. 1991), our findings suggest the possibility of unimodal relationships between generalist predator density and the cyclicity of prey populations. This type of relationship may result because a predator exhibiting a type-II functional response has its strongest impacts on low-density prey populations. If the density of such a predator is moderate, the predator population can deepen the population crashes of their prey, which may enhance the amplitude of prey cycles. If the predator population is sufficiently dense, however, the resulting Allee effect may be strong enough to disrupt prey population cycles since recovery following a population crash would be strongly hampered.

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