

Research

Geographic variation in forest composition and precipitation predict the synchrony of forest insect outbreaks

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Oikos

127: 634–642, 2018

doi: 10.1111/oik.04388

Subject Editor: Thorsten Wiegand

Editor-in-Chief: Dries Bonte

Accepted 20 October 2017

Evaluating the causes of spatial synchrony in population dynamics in nature is notoriously difficult due to a lack of data and appropriate statistical methods. Here, we use a recently developed method, a multivariate extension of the local indicators of spatial autocorrelation statistic, to map geographic variation in the synchrony of gypsy moth outbreaks. Regression analyses indicated that local synchrony of gypsy moth defoliation increased with the local synchrony of precipitation and the proportion of host tree density composed of oaks, especially those in the *Lobatae* (red oak) section. This may be the first study that demonstrates a relationship between defoliator population synchrony and host tree composition. More broadly, this study contributes to a small body of recent work that illustrates how mapping hotspots of unusually high or low synchrony facilitates an improved understanding of factors influencing spatially synchronous population dynamics generally, and triggers of pest insect outbreaks, more specifically.

Introduction

Spatial synchrony of fluctuations in abundance is widespread among animal taxa (e.g. mammals, birds, fish and insects) and is observable across hundreds of kilometers (Liebhold et al. 2004). Traditionally, spatial synchrony among animal populations of a focal species has been thought to be caused by dispersal among populations (either by the focal species or by its mobile predators) or regionally synchronous environmental impacts acting directly on population growth (Haydon and Steen 1997, Kendall et al. 2000). In addition, some recent studies provide compelling evidence of synchronization of a species populations' via trophic interactions with another species that fluctuates synchronously (Satake et al. 2004, Cattadori et al. 2005). Factors that can diminish the synchronizing effects of these drivers of synchrony include differences

between locations in density-dependent population dynamics and barriers to dispersal (Walter et al. 2017).

For most species, outside of those studied in experimental microcosms (Vasseur and Fox 2009, Duncan et al. 2015), it is difficult to determine which of the factors described above (alone or in combination) are driving or inhibiting the synchrony of spatially isolated populations (Haynes et al. 2009). Experimental tests of synchronizing factors are often not practical for a variety of reasons including the long generation times of many species and the large distances over which synchronous population fluctuations occur (Peltonen et al. 2002). Historically, additional hurdles to the study of population synchrony included the rarity of population abundance datasets that were both temporally and spatially extensive and a lack of well-developed statistical approaches appropriate for spatially structured time-series data (Koenig 1999).

Many studies have investigated the spatial synchrony of animal abundances or mast seed production by measuring the region-wide average strength of synchrony as a function of distance between sampled locations (Hanski and Woiwod 1993, Haynes et al. 2009, Nieminen 2015). However, this approach fails to capture information about the drivers and inhibitors of synchrony that can be gleaned from spatial heterogeneity in the strength of synchrony (Walter et al. 2017). Multiple regression of pairwise resemblance matrices (MRM; Manly 1986, Legendre and Legendre 1998, Lichstein 2007) is one approach that has been used to isolate the importance of different potential drivers of synchrony (Drever 2006, Haynes et al. 2013). For example, using MRM, Haynes et al. (2013) found the synchrony of outbreaks of a foliage-feeding insect, the gypsy moth *Lymantria dispar*, in North America was best explained by the synchrony of precipitation. After accounting for the synchrony of precipitation, no other factors, including the proximity of locations, were significantly associated with the synchrony of gypsy moth outbreaks (Haynes et al. 2013). It was concluded that dispersal was unlikely to be a driver of the synchrony of gypsy moth populations and that synchrony in precipitation could synchronize gypsy moth populations directly (e.g. via a Moran effect) or indirectly through effects on gypsy moth predators (mainly small mammals) or viral (the gypsy moth nucleopolyhedrosis virus; *LdNPV*) or fungal (*Entomophaga maimaiga*) pathogens (Haynes et al. 2013).

Though MRM may continue to be an important tool for statistically partitioning the sources of population synchrony, the value of this procedure is limited in at least two ways. First, spatial structure in MRM is distilled into one dimension: distance (or conversely, proximity). Second, the data used in MRM must be measures of similarity or dissimilarity between locations, rather than using specific conditions at each location. Consequently, effects of the actual magnitude of a given variable (e.g. low to high-density of host trees) on synchrony cannot be assessed.

Here, we apply a recently developed method for mapping and statistically analyzing the two dimensional spatial structure of synchrony – the non-centered local indicators

of spatial autocorrelation, (ncLISA; Gouveia et al. 2016) – to improve our understanding of the factors synchronizing gypsy moth outbreaks in North America. We used ncLISA to measure synchrony of gypsy moth defoliation within local neighborhoods. We then used spatial regression to evaluate the extent to which the local synchrony of gypsy moth defoliation may be influenced not only by the synchrony of weather variables (Haynes et al. 2013), but also by the densities of particular groups of gypsy moth host trees. Across the gypsy moth's range in North America, red oaks (section *Lobatae*) and white oaks (section *Quercus*) are this folivore's most abundant hosts (Liebhold et al. 1997). These two sections of oak may have differential effects on gypsy moth synchrony owing to differences in the importance of their acorns to the population dynamics of small mammal species that are both acorn predators and opportunistic predators of gypsy moth pupae (Haynes et al. 2009, 2013). Oaks in both sections exhibit spatially synchronous production of large acorn crops (Fearer et al. 2008), a phenomenon known as mast seeding, however, only red oak acorns provide a major winter food supply for small mammal predators (Fox 1982, Hadj-Chikh et al. 1996, Elkinton et al. 1996, Steele et al. 2001, Elias et al. 2004, Shimada and Saitoh 2006). Given the importance of red oak acorns to the population dynamics of small mammal predators, it is possible synchrony in red oak acorn production could be transferred trophically from acorns to predator populations and, in turn, from predators to gypsy moth populations (Haynes et al. 2009). Haynes et al. (2013) found no significant relationship between the similarity of 'forest type groups' (e.g. oak-hickory, maple-beech-birch) and the synchrony of gypsy moth outbreaks. However, forest type groups (Ruefenacht et al. 2008) are coarse categorizations of tree-species assemblages, and measurements of similarity in forest type groups provide no information about the contributions of particular host tree taxa to the synchrony of gypsy moth populations. In contrast to examining associations between the synchrony of gypsy moth outbreaks and the similarity of forest type groups as in Haynes et al. (2013), in this study we examined associations between gypsy moth synchrony and the proportion of preferred host trees composed of particular tree taxa. Specifically, we examined associations between the synchrony of gypsy moth defoliation and the proportion of the basal area of preferred host tree species (Liebhold et al. 1995) composed of red oaks, white oaks, or preferred host species other than oaks (dominated by birches and aspens), while accounting for the synchrony of temperature and precipitation.

Methods

Study system

Following its introduction from Europe into North America in the 1860s, and subsequent range expansion, gypsy moth populations in North America have exhibited recurring outbreaks resulting in defoliation of large swaths of forest

(Liebhold et al. 2000). These outbreaks have occurred with statistically significant cyclicity at intervals of approximately 4–5 and 8–10 years (Johnson et al. 2006) and moderate spatial synchrony over distances up to ~900 km (Peltonen et al. 2002, Haynes et al. 2009).

The gypsy moth has a broad host range, feeding on over 200 tree species in North America, but displays strong preferences for particular taxa (Liebhold et al. 1995). This insect's preferred host species, those scored with the highest ranking based on laboratory and field studies (Liebhold et al. 1995), are found in a variety of genera including oaks (*Quercus*), aspens (*Populus*), birches (*Betula*), hawthorns (*Crataegus*), alders (*Alnus*) and willows (*Salix*).

Defoliation, host tree composition and weather data

We quantified geographic variation in the spatial synchrony of gypsy moth defoliation across 453 632 km² over a 40 year period (1975–2014) in the northeastern US based on an archive of aerial survey maps. Each yearly map was digitized and stored in a geographic information system in raster format; Liebhold et al. (1997) and Johnson et al. (2006) contain additional information on the methods used to quantify defoliation. The area (km²) of forest defoliated within a given 32 × 32 km quadrat was used as a proxy of local gypsy moth abundance. The defoliation data have a maximum resolution of 2 × 2 km, however, we chose to use the 32 × 32 km quadrats to facilitate testing of relationships between defoliation and host tree composition. To ensure gypsy moths were established in all quadrats over the entire study period, we limited our study to locations within the 1974 'generally infested area' according to US Dept of Agriculture gypsy moth quarantine regulations (US Code of Federal Regulations, title 7, ch. III, §301.45).

Area of forest defoliated is positively correlated with gypsy moth density (egg masses ha⁻¹; Williams et al. 1991, Liebhold et al. 1993). However, defoliation data are of limited value for tracking fluctuations in low-density gypsy moth populations, as the threshold for detection of defoliation is ~30% defoliation (Ciesla 2000). Quadrats within the 'generally infested area' where defoliation was detected typically support low gypsy moth densities, thus including them in our analysis would introduce a high degree of measurement error. To reduce potential biases introduced by such error, we excluded quadrats where defoliation was detected in fewer than five years across the 40-year study period.

Geographic variation in the density of red oaks, white oaks, and other highly preferred host trees (Liebhold et al. 1995) was determined using data from the US Forest Service Forest Inventory and Analysis Program (FIA) (Bechtold and Patterson 2005). The densities of these host trees were estimated based on basal areas per unit area (m² ha⁻¹). Across the quarantined study area a total of 20 684 FIA plots were surveyed from 2009–2013.

We deemed that ≥ 10 FIA survey plots were needed within each quadrat to adequately characterize tree species composition, and then selected the finest resolution that would allow

a majority of quadrats meet the criterion. This led to our selection of the 32 × 32 km resolution. Sixty-four of the 443 quadrats did not contain ≥ 10 FIA survey plots and were thus excluded from further analysis. Of the remaining 379 quadrats, 253 (259 072 km²) met our criterion of being defoliated by gypsy moths ≥ 5 times. We gathered monthly weather data for each of these quadrats from the PRISM Climate Group (<<http://prism.nacse.org>>). From these weather data, we obtained total precipitation, and the means of daily minimum and maximum temperature, for each month (Jan–Dec) across each year (1975–2014). This resulted in 40 year-time series for each of 36 weather variables (3 weather variables across 12 months). Each variable was scored at a resolution of 1 × 1 km and then averaged across each 32 × 32 quadrat. Given the large number of variables involved, many collinear, we used principal components analysis (PCA) to characterize variation in weather based on a smaller number of dimensions. We selected two dominant components (Supplementary material Appendix 1 Fig. A1) with which to evaluate the spatial synchrony of weather. The principal components analysis was carried out using the 'stats' package for the R language (<www.r-project.org>). All statistical analyses in this paper were performed using R.

Analysis of spatial synchrony

We measured the spatial synchrony of defoliation and two weather components at a local scale (among neighboring 32 × 32 km quadrats) using Gouveia et al.'s (2016) multivariate extension of the local indicators of spatial autocorrelation (LISA) statistic (Anselin 1995). In contrast to global measures of spatial autocorrelation such as Moran's *I* or Geary's *c*, the LISA statistic, for a given observation taken from a single location, is a measure of the similarity of values in a neighborhood around each spatial location (Anselin 1995). The LISA statistic accommodates a single observation at each location (Anselin 1995), thus it allows identification of hotspots (and coldspots) of spatial autocorrelation from a snapshot in time. Gouveia et al.'s (2016) multivariate LISA statistic (ncLISA) allows repeated observations of the same variable (i.e. time series) at each location. This statistic is a measure of the synchrony (correlation through time) of observations between a given location and locations within a local neighborhood. As with many previous methods of studying spatial synchrony, pairwise synchrony among any two locations *i* and *j* is quantified with the Pearson correlation coefficient $\rho_{ij} = \sum_i \frac{(y_{i,t} - \mu_i)(y_{j,t} - \mu_j)}{\sigma_i \sigma_j}$ and the 'non-centered' label is in the spirit of Koenig (1999), for which the measure of synchrony is not centered on the region-wide average (Bjørnstad et al. 1999). As with the LISA statistic, a neighborhood size is specified by choosing a maximum distance from a given focal location beyond which pairwise synchrony measures are not included in the locally-averaged measure of synchrony. The ncLISA statistic for location *i* is thus $\frac{1}{|\Omega_i|} \sum_{j \in \Omega_i} \rho_{ij}$, where Ω_i denotes the set of *j* locations that belongs to the neighborhood

of i and $|\Omega_i|$ is the number of locations in the neighborhood. Statistical significance is ascertained using a randomization test under the null hypothesis of no spatial structure to the variation in synchrony; under the null hypothesis the time series are thus permuted among locations and the statistic is recalculated.

We performed this analysis on the defoliation and weather data using the nCLISA function in the 'ncf' package (Bjørnstad 2016) for R. We used a neighborhood size consisting up to eight nearest neighboring quadrats (as permitted by our quadrat selection criteria).

Next, we used spatial regression (below) with an information-theoretic approach (Burnham and Anderson 2002), consisting of ranking models based on AIC_c values, to find parsimonious models for predicting the local synchrony of gypsy moth defoliation. Following Burnham and Anderson (2002), models with ΔAIC_c values < 2 were deemed to have similar support. The set of candidate models considered included a full model with the predictor variables: proportion of host basal area composed of red oaks (RO), proportion of host basal area composed of white oaks (WO), and the synchronies in the scores of the two dominant weather components (S_1 and S_2). We used the proportions of preferred host basal area composed of red or white oaks rather than simply the basal areas of each oak section to control for differences in total host basal area (including hosts other than oaks) among quadrats. The proportion of hosts other than oaks was not included as a predictor variable because this would introduce perfect multicollinearity (this variable is $1 - RO - WO$).

The other models within the candidate set contained 0-3 of the four predictor variables in all possible combinations. An intercept term was fitted for all models. The model with an intercept term but no predictor variables, the 'intercept-only' model, was fitted and treated as a candidate model.

All candidate models were specified as weighted generalized least squares (GLS) regressions to account for spatial

autocorrelation and differences in sample size (number of quadrats per neighborhood). To account for spatial autocorrelation, we evaluated the spatial structure present in the residuals of a full model (i.e. containing all predictor variables) and chose the type of function (Gaussian, exponential or no spatial structure) to use for modeling how spatial autocorrelation decays with respect to distance among quadrats based on AIC_c values. The weight of each focal quadrat was taken as the number of quadrats in its neighborhood. The GLS regressions were conducted using the 'nlme' package (Pinheiro et al. 2016). A power transformation, $f(x) = x^t$ (Tukey 1977, Williamson and Gaston 1999), with $t = 2.1$ was applied to the local synchrony values to optimize the normality of the GLS model residuals. The full model was checked for multicollinearity by calculating the variance inflation factors of each predictor variable.

Data deposition

Data available from the Knowledge Network for Biocomplexity Repository: <https://knb.ecoinformatics.org/#view/Blandy.334.9> (Haynes et al. 2017).

Results

Using the FIA survey plot data, we found red oaks were the dominant group of host trees relative to other groups in the central and much of the northeastern portion of the study area (Fig. 1a). In contrast, white oaks tended to be dominant host trees only in the southern part of the study area (Fig. 1b). Preferred host tree species that were not oaks dominated only the extreme northern and northwestern margin of the study area (Fig. 1c). Overall, 44.4% of the host tree basal area in our study area was comprised of red oak species and 36.1% was white oak species. Preferred host tree species other than oaks were dominated by birches (*Betula*) and

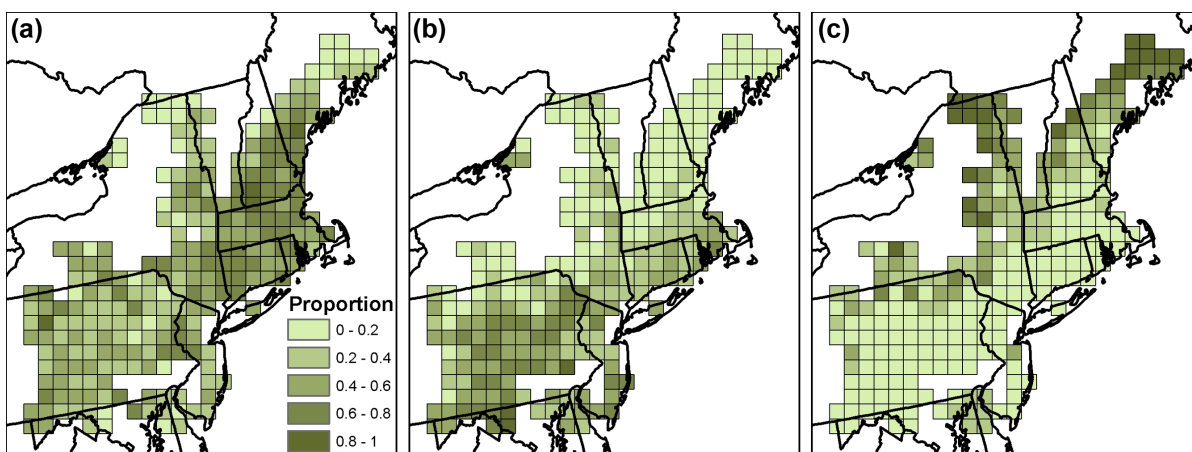


Figure 1. (a) Maps of the proportion of preferred host tree basal area composed of red oak species, (b) white oak species, and (c) non-oak preferred host species derived from 2009–2013 survey data gathered by the Forest Inventory and Analysis Program (Bechtold and Patterson 2005).

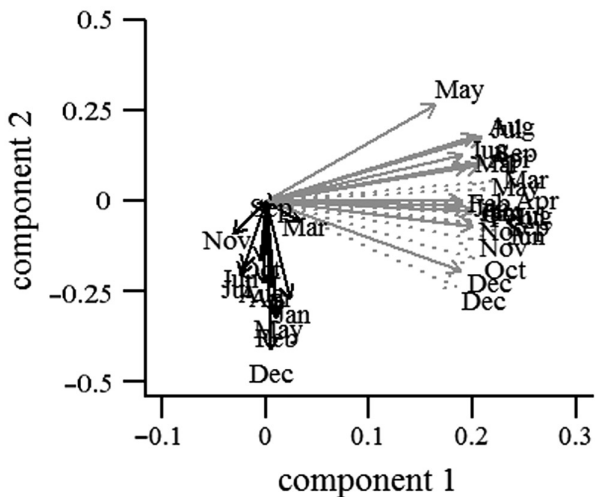


Figure 2. Biplot of principal components analysis of monthly measures of total precipitation and mean minimum and maximum temperatures from 1975–2014 across the study area locations. The precipitation variables are displayed with solid black lines. Mean minimum and maximum temperatures are shown with solid and dotted gray lines, respectively.

aspens (*Populus*), which made up 7.2% and 6.7% of the total preferred host species basal area, respectively.

Using principal components analysis (PCA) we characterized variation in 36 monthly weather variables (total precipitation, mean minimum temperature, and mean maximum temperature) across the 40-year time series. The temperature variables largely loaded onto the first principal component (PC), whereas the precipitation variables loaded most strongly on the second PC (Fig. 2). The first and second PCs explained approximately 52% and 8% of the variation in the weather variables, respectively.

The nCLISA analysis revealed that the scores of the first PC, largely representing temperature, tended to be most

spatially synchronous in the mid and lower latitudes of the study area (Fig. 3a). The scores of the second PC, largely representing precipitation, were most synchronous in the southern and the extreme northeastern portion of the study (Fig. 3b). For both PC's, local synchrony was high throughout the study region. Generally, gypsy moth defoliation was most strongly synchronous in the northeastern part of the study area, with the exception of the quadrats within 64 km of the extreme northern edge (Fig. 3c).

Among the 16 candidate GLS regression models for predicting geographic variation in the local synchrony of gypsy moth defoliation only three received substantial support ($\Delta AIC_c < 2$) (Table 1). All three of these models fit the data moderately well ($r^2 = 0.56$). Red oak density (RO) and the synchrony of the second PC (S_2) were present in all three of the selected models and in all of these models both variables had positive relationships with the synchrony of gypsy moth outbreaks (Table 1). White oak density (WO) was a predictor in two of the selected models, with increasing WO associated with higher synchrony of outbreaks, though the regression coefficients for RO (0.17 ± 0.06 ; coefficient ± 1 SE) were somewhat larger than those for WO (0.09 ± 0.05) in the two models where both variables occur (Table 1). Both variables are proportions, which vary on the same scale (0–1), making comparisons of their regression coefficients straightforward. Only one model containing S_1 was selected. In this model, there was a negative relationship between S_1 and the synchrony of gypsy moth outbreaks, though the confidence interval contains zero. The selected model containing S_1 also contained S_2 , both of which are correlation coefficients with the potential to range from –1 to 1. Based on the regression coefficients in the model containing both variables, the impact on the synchrony of gypsy moth defoliation of a change of a given size in S_2 would be substantially greater than a change of the same size in S_1 (Table 1). The best spatial decay model for the regression residuals was the Gaussian autocorrelation function (as

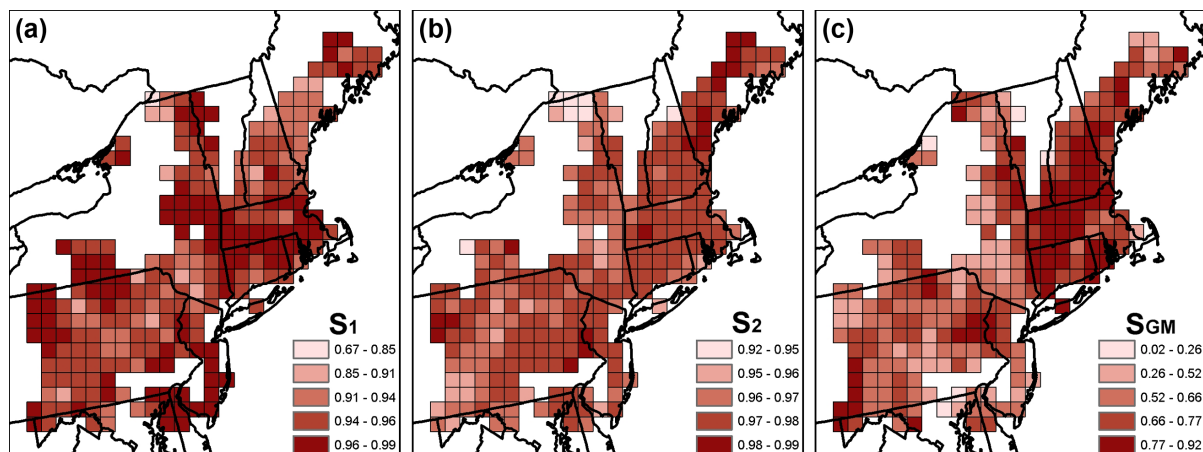


Figure 3. (a) Local synchrony in the first weather PC (S_1), (b) second weather PC (S_2), and (c) gypsy moth defoliation (S_{GM}) determined from non-centered local indicators of spatial autocorrelation (nCLISA) analysis. Darker red coloring indicates increasingly strong local synchrony. The color ranges vary among panels.

Table 1. The highest ranking generalized least squares regression models for predicting the local synchrony of gypsy moth defoliation based on host-tree composition (proportions of host basal area composed of red [RO] or white oaks [WO]) and the synchrony of the first (S_1) and second principle components (S_2) of the monthly weather variables. The set of candidate models considered consisted of a global model with the predictor variables RO, WO, S_1 and S_2 , and reduced models with predictor variables removed in all possible combinations, including an ‘intercept-only model’ with all predictor variables removed. The AIC_c weight for a given model indicates the probability it is the most parsimonious model.

Model rank	Coefficients \pm 1 SE				ΔAIC_c^*	AIC_c weights	r^2
	RO	WO	S_1	S_2			
1	0.17 \pm 0.06	0.09 \pm 0.05		2.79 \pm 1.24	0	0.34	0.56
2	0.14 \pm 0.05			3.07 \pm 1.23	0.86	0.22	0.56
3	0.17 \pm 0.06	0.09 \pm 0.05	-0.24 \pm 0.38	3.06 \pm 1.31	1.72	0.14	0.56

*Only models with $\Delta AIC_c < 2$ are shown.

opposed to an exponential function or no autocorrelation) according to the AIC_c . Multicollinearity in the full model was low; the highest variance inflation factor value was 1.38.

Discussion

One of the main obstacles that has historically stood in the way of identifying drivers of population synchrony has been a lack of statistical methods for examining spatiotemporal relationships. However, the accessibility of these methods to many ecologists, has generally been increasing in recent years. The availability of methods for evaluating the explanatory power of multiple environmental factors from spatially structured data (Manly 1986), as well as methods for quantifying the spatial clustering of synchrony (Gouveia et al. 2016), may make one of the main previous approaches – comparing the region-wide distance–decay of synchrony of populations with that of environmental factors – obsolete. The MRM approach is more powerful than evaluation of distance-day relationships because it uses the information inherent in any spatially-explicit variation in population synchrony and other similarity variables (e.g. the synchrony of weather variables). The former approach (comparison of distance–decay relationships) averages across any spatial structuring of synchrony patterns within the study region (and suffers from how different mechanisms can give rise to similar distance–decay patterns), whereas the latter exploits the spatial structuring of synchrony to better distinguish among synchronizing agents. The pairwise nature of MRM, unlike the nCLISA approach used here, however, is not suited for identifying regional hotspots (neighborhoods) of unusually high or low spatial synchrony, again because it averages across spatial heterogeneities.

We believe the ability of the nCLISA approach to explicitly define (significant) areas of unusually high or low spatial synchrony will make it a useful tool in future empirical exploration of the drivers of spatial synchrony. Once heterogeneity in synchrony has been mapped, a broad array of spatial regression techniques can be used to evaluate relationships between spatial synchrony and geographically varying factors. Walter et al. (2017), recently further suggested

local measures of synchrony may be combined with network algorithms to cluster non-neighborhood quadrats. With the statistical barriers to the study of spatial synchrony substantially lowered, lack of spatiotemporal data will likely become the main remaining challenge to the field. For those organisms for which extensive spatiotemporal datasets already exist however, we recommend re-examining the potential drivers of population synchrony using the newly available tools.

Our nCLISA analysis revealed that synchrony of gypsy moth outbreaks increased with the proportions of host tree basal area composed of red oaks and white oaks and the synchrony of precipitation (Table 1). The increase in the synchrony of gypsy moth outbreaks across a spatial gradient of increasing synchrony of precipitation is consistent with the findings of Haynes et al. (2013) using a MRM approach. Here, we note that small differences in the strength of precipitation synchrony were associated with geographic variation in synchrony of gypsy moth populations (Table 1) given that the synchrony of precipitation was high throughout the study area (Fig. 3b).

There are a number of potential explanations for why gypsy moth populations are more synchronous in areas with higher local synchrony in precipitation. One explanation is that precipitation synchronizes gypsy moth population fluctuations through a Moran effect, i.e. direct impacts of precipitation on gypsy moth survival or reproduction bring its populations into synchrony. Alternatively, precipitation may synchronize gypsy moth populations by promoting synchrony in pathogen transmission rates, mirroring the synchronization of red grouse populations in England resulting from the influence of weather conditions on parasite infection rates (Cattadori et al. 2005). The gypsy moth is affected by two major pathogens in the study area, the gypsy moth nucleopolyhedrosis virus (*LdNPV*) and the fungus *Entomophaga maimaiga*. In a previous artificial watering experiment, D’Amico and Elkinton (1995) showed that rainfall can transfer the virus among branches. Given that the gypsy moth becomes infected by consuming leaves coated in virus particles, increased spread of viruses through tree canopies due to rainfall could increase rates of infection. In addition, rates of infection by *Entomophaga maimaiga* are known to increase with precipitation that falls during gypsy moth’s susceptible

larval stages (Weseloh et al. 1993, Hajek and Tobin 2011). *Entomophaga maimaiga* was largely absent from North America until 1989, so further studies of how precipitation synchrony affects gypsy moth synchrony directly or differentially via the two pathogens will be necessary for detailing the exact mechanisms whereby spatially synchronous precipitation promotes outbreak synchrony.

The increase in synchrony in gypsy moth outbreaks with increasing proportions of red oaks (RO) and white oaks (WO; Table 1) indicates synchrony is lower in areas dominated by other preferred host tree species (mainly birches and aspens). Using MRM, Haynes et al. (2013) and Walter et al. (2017) found no relationships between forest type group similarity and the synchrony of gypsy moth outbreaks. Potential explanations for why tree species composition was a useful predictor of gypsy moth synchrony in the present study, but the previous studies found no effects of forest type group similarity, are not entirely clear. However, the fact that the present study focused exclusively on preferred host tree species, whereas the previous studies used broad categorizations of tree assemblages (forest type groups) reflecting the composition both host and non-host tree species, may be important. Lower relevance of non-host species than host species to gypsy moth population dynamics may explain why relationships between tree species composition and gypsy moth synchrony were not found prior to this study. In addition, unlike the MRM approach used by Haynes et al. (2013) and Walter et al. (2017), the statistical approach used here did not require the predictors to be similarity (or dissimilarity) matrices. The generation of a two-dimensional map of the strength of synchrony using nCLISA allowed us to better evaluate whether the strength of synchrony varied in response to gradients in host tree densities.

Why host tree species composition is a predictor of local synchrony among gypsy moth populations while it is seemingly unrelated to typical drivers of spatial synchrony in animal population fluctuations (dispersal or spatially synchronous environmental fluctuations) should be considered. Walter et al. (2017) reviewed how factors generating spatial structure in the strength of synchrony need not be synchronizing factors themselves. One mechanism that likely plays a role in creating spatial variability in the strength of population synchrony is spatial heterogeneity in density dependent population regulation; heterogeneity among locations in population regulation likely degrades the synchrony of population fluctuations (Peltonen et al. 2002, Liebhold et al. 2006). In this study, we only considered highly preferred host tree species, nonetheless differences in the species composition of these host trees may influence gypsy moth population regulation. For example, host plant composition is known to influence the susceptibility of gypsy moth larvae to the gypsy moth nucleopolyhedrosis virus (*LdNPV*) (Keating and Yendol 1987), which causes density-dependent mortality (Woods and Elkinton 1987).

We can think of at least two potential explanations for why gypsy moth outbreaks were more locally synchronous

in areas with high densities of oaks, and especially red oaks (Table 1). First, if defoliator population dynamics are affected by host species composition, a defoliator population at a focal location may be most synchronous with populations in surrounding locations if the focal population occurs in an area dominated by the host species that is the most regionally abundant. In the eastern United States, red oaks are more common than white oaks, which, in turn, are more common than any other group of the gypsy moth's highly preferred host species (Fig. 1). This trend in host tree abundance mirrors the trend in the strength of synchrony of gypsy moth populations; the synchrony of gypsy moth populations increased with the dominance of oaks (especially red oaks) and decreased as host trees were increasingly composed of species other than oaks (Table 1). Alternatively, host tree species composition (particularly red oak density) may influence gypsy moth synchrony by affecting the synchrony of gypsy moth predator populations. Predation of gypsy moth pupae during the summer by small mammals, especially the white-footed mouse *Peromyscus leucopus*, is one of the main factors influencing the growth of gypsy moth populations while gypsy moth densities are low (Elkinton and Liebhold 1990, Elkinton et al. 1996). White-footed mouse densities tend to crash approximately every 4–6 years (Wolff 1996, Elias et al. 2004), in part, because of the mast seeding (cyclical seed production) of red oak acorns, which serve as a critical winter food source for these rodents (Wolff 1996, Elkinton et al. 1996, Jones et al. 1998, Elias et al. 2004, Clotfelter et al. 2007). Declines in white-footed mouse densities following low production of red oak acorns is thought to reduce predation of gypsy moth pupae (Elkinton and Liebhold 1990, Elkinton et al. 1996). Red oak acorns are well suited for provisioning caches of winter food because they are typically produced in autumn but delay germination until the following spring (Hadj-Chikh et al. 1996). In contrast, white oak acorns germinate in the autumn soon after seed fall (Fox 1982) and they are only occasionally cached by small mammals (successful caching of a white oak acorn requires prevention of germination by excising the embryo; Steele et al. 2001). Red oak acorn production and densities of the white-footed mouse and gypsy moths fluctuate synchronously over similar distances (Haynes et al. 2009). Using an empirically informed simulation model, Haynes et al. (2009) showed that trophic interactions could transfer the spatial synchrony of red oak acorn production to white-footed mouse populations and, in turn, gypsy moths. However, direct empirical evidence that trophic interactions underlie the similar patterns of synchrony in these species is lacking. It is also unclear if higher densities of red oak trees (and thus higher densities of red oak acorns) would increase the synchronizing effects of small mammal predation on gypsy moth populations. Thus, further critical evaluation of this hypothesis is warranted. The study of geographic variation in the synchrony of population fluctuations will likely play an important role in future discoveries of synchronizing and desynchronizing factors.

Acknowledgements – We thank Ariel Firebaugh, Melissa Hey and Thorsten Wiegand for helpful comments on earlier drafts of this manuscript and E. Luzader for assisting with data compilation. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service.

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Supplementary material (available online as Appendix oik-04388 at <www.oikosjournal.org/appendix/oik-04388>). Appendix 1.