

# Temporal variation in the synchrony of weather and its consequences for spatiotemporal population dynamics

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**Abstract.** Over large areas, synchronous fluctuations in population density are often attributed to environmental stochasticity (e.g., weather) shared among local populations. This concept was first advanced by Patrick Moran who showed, based on several assumptions, that long-term population synchrony will equal the synchrony of environmental stochasticity among locations. We examine the consequences of violating one of Moran's assumptions, namely that environmental synchrony is constant through time. We demonstrate that the synchrony of weather conditions from regions across the United States varied considerably from 1895 to 2010. Using a simulation model modified from Moran's original study, we show that temporal variation in environmental synchrony can cause changes in population synchrony, which in turn can temporarily increase or decrease the amplitude of regional-scale population fluctuations. A case study using the gypsy moth (*Lymantria dispar*) provides empirical support for these predictions. This study provides theoretical and empirical evidence that temporal variation in environmental synchrony can be used to identify factors that synchronize population fluctuations and highlights a previously underappreciated cause of variability in population dynamics.

**Key words:** gypsy moth; *Lymantria dispar*; Moran effect; periodicity; population model; regional stochasticity; spatial coherence; spatial synchrony; wavelet analysis; wavelet coherence.

## INTRODUCTION

A wide variety of species exhibit synchronous fluctuations in the density of spatially disjunct populations (Hanski and Woiwod 1993, Liebhold et al. 2004). This spatial synchrony, hereafter “population synchrony,” implies that the behaviors of local populations are interrelated over larger areas (Ranta et al. 1997). High levels of population synchrony mean that local population densities change in unison, causing high amplitude fluctuations in regional (system-wide) population density (Heino et al. 1997, Liebhold et al. 2012). Highly synchronous dynamics can increase the risk of extinction for rare species, as there can be no rescue effect if all population densities are simultaneously low (Heino et al. 1997, Abbott 2011). Conversely, synchronous cycles in population density may allow outbreaking pest species to escape regulation by mobile natural enemies and increase the severity of damage (Liebhold et al. 2012). Consequently, understanding patterns and drivers of population synchrony may improve our ability to assess risks to species, whether the focus is conservation or pest management.

A general result from theoretical models of spatio-temporal population dynamics is that fluctuations of spatially disjunct populations can be synchronized through relatively weak interactions among populations, such as coupling (e.g., dispersal) or common forcing (e.g., shared environmental disturbance). A special case of shared forcing of particular interest in ecology is the Moran effect (Royama 1992). This phenomenon is named for Patrick Moran, who found that the asymptotic synchrony of populations governed by identical log-linear, density-dependent dynamics will equal the level of synchrony in environmental disturbances (Moran 1953, Royama 1992). Weather is often thought to provide this synchronizing disturbance, given its potential effects on birth/death processes and its consistent synchrony over spatial scales similar to population synchrony (Moran 1953, Koenig 2002). The Moran model has been extended to incorporate systems with nonlinear (Ranta et al. 1997, Engen and Sæther 2005) and spatially heterogeneous population dynamics (Peltonen et al. 2002, Engen and Sæther 2005, Liebhold et al. 2006), and to include dispersal (Ranta et al. 1998, Kendall et al. 2000). However, although there is evidence that synchrony of weather conditions can change through time (Walsh et al. 1982, Haston and Michaelsen 1997), effects of this type of temporal variation on ecological processes have not been explored.

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Though the Moran effect predicts a long-term equality between environmental and population synchrony, population synchrony is known to vary over shorter timescales (Ranta et al. 1998). A few studies have linked this variation to anomalous mean weather conditions (Forchhammer et al. 2002, Haydon et al. 2003, Cattadori et al. 2005), but we found only two studies that examined temporal variation in both environmental and population synchrony. Post and Forchhammer (2004) linked a long-term, increasing trend in the synchrony of winter temperatures to increases in the population synchrony of caribou in Greenland. In contrast, Jepsen et al. (2009) examined short-term changes in synchrony during an outbreak of Fennoscandian geometrid moths. They observed that both environmental and population synchrony were high during the incipient phase of an outbreak, and then both decreased as the outbreak progressed. Interestingly, they also suggest that this temporary high level of population synchrony led to an unusually widespread outbreak of these moths. However, verifying that short-term changes in environmental synchrony can alter population synchrony, and subsequently increase the amplitude of regional outbreaks, would require a theoretical basis and examination of empirical data spanning more than one population cycle.

The goal of our study is to extend Moran-effect theory to include temporal variation in environmental synchrony. We begin by demonstrating that a commonly cited source of environmental synchrony, the synchrony of weather, varies substantially through time in regions throughout the USA. Next, we incorporate temporal variation in environmental synchrony into Moran's original model, which captures the population dynamics of a wide variety of animals. Using this model, we determine conditions under which temporal variation in environmental synchrony can affect population synchrony and the amplitude of regional population fluctuations. Finally, we test these theoretical predictions in an empirical case study of the gypsy moth (*Lymantria dispar*). This is an ideal system to test these predictions because, although little is known about temporal variation in environmental or population synchrony in this system, there is strong evidence that weather synchronizes gypsy moth outbreaks (Peltonen et al. 2002, Haynes et al. 2013), and extensive spatiotemporal datasets are available.

## METHODS

### *Temporal patterns in the synchrony of weather*

Study of temporal variation in the Moran effect makes sense only in light of temporal variation in environmental synchrony, so we began by characterizing changes in the synchrony of weather conditions through time. We calculated synchrony in interannual variation in monthly precipitation totals and monthly averages of both minimum and maximum daily temperatures from 1895 to 2010, based on readings from 1218 first-order

weather stations in the U.S. Historical Climatology Network across the 48 conterminous states of the USA (National Climatic Data Center (NCDC); data *available online*).<sup>6</sup> To explore geographic consistency in patterns of synchrony of weather, we divided these weather stations into the nine NCDC climatic regions: the Northeast, Upper-Midwest, Ohio Valley, Southeast, South, Southwest, West, and Northwest. We treated each variable, region, and month separately, for a total of 324 time series. Prior to synchrony calculations, we removed a mild positive skew from the precipitation totals with a square root transformation.

Synchrony between two sites is generally calculated in a time-invariant manner as the correlation among measurements for the entire length of the time series, though some previous studies have calculated correlations within moving windows of 10 or more years to examine changes in the synchrony of weather through time (e.g., Ranta et al. 1998, Post and Forchhammer 2004, Bjørnstad et al. 2008). To maximize temporal resolution and minimize autocorrelation, we measured synchrony within even shorter 3-yr moving windows. For each time window, we calculated all pairwise correlations among locations and reported the mean of these pairwise correlations as synchrony for the middle year of that time window (Appendix A). Averaging over  $n(n-1)/2$  pairwise correlations, where  $n$  was the number of locations in the region, helped reduce noise from stochastic phase slip among oscillations at individual locations (Appendix A). The minimum possible value of these average correlations is  $-1/(n-1)$  given a constant variance among locations, so that anti-synchronous states become less likely as the sample size increases (Gouhier and Guichard 2014). Alternative concordance measures of synchrony do not suffer from this contraction, but range only from 0 to 1 and require a second step to determine if a given value is synchronous or anti-synchronous (Gouhier and Guichard 2014). Concordance measures also performed poorly in our zero-heavy gypsy moth defoliation records. Interestingly, the mean correlations coefficient and concordance techniques both indicated few negative values and these negative were typically close to zero (data not shown).

The temporal scale of fluctuations in the synchrony of weather may influence how these fluctuations affect ecological processes. For example, annual fluctuations in the synchrony of weather might have less of an effect than longer term changes. Initial visual inspection of changes in the synchrony of weather conditions through time revealed apparent periodic behavior, one form of longer term changes. To inform our simulation model and statistical analyses, we evaluated the extent of periodicity in the synchrony of weather conditions using wavelet analysis (Torrence and Compo 1998, Cazelles et al. 2007). The continuous wavelet transform is similar to

<sup>6</sup> [www.ncdc.noaa.gov/data-access/land-based-station-data](http://www.ncdc.noaa.gov/data-access/land-based-station-data)

Fourier analysis in that it breaks down a time series into its cyclical components but has the additional feature of characterizing temporal variation in periodicity (Torrence and Compo 1998; details in Appendix B). The wavelet transform is a convolution of the time series with a wavelet function, a periodic function resolved in time and an adjustable cycle length. Repeating this convolution for all time steps and frequencies provides the ability to detect temporal variability in periodic behavior, as displayed in the wavelet spectrum. We conducted these analyses using a Matlab package that applies the widely used Morlet wavelet (Cazelles et al. 2007) modified to correct a bias towards low-frequency signals inherent to traditional wavelet analysis (Liu et al. 2007). While the wavelet transform does not require that a time series follow a specific distribution, the Morlet wavelet itself is normally distributed, and normally distributed data often produce more reliable results (Jevrejeva et al. 2003, Grinsted et al. 2004). We improved the normality of these time series with the Box-Cox transform (Box and Cox 1964), using the Matlab function `boxcox` to determine the maximum likelihood value of the transformation parameter. The time series were then transformed to a standard normal distribution. We tested for significant periodicity using a hidden Markov model simulation experiment, which accounts for short-term autocorrelation present in the time series, without making assumptions about the structure of that autocorrelation (Cazelles et al. 2014).

#### Simulation model

Moran's original work demonstrated that, over the long term, synchrony among local populations was equal to the level of environmental synchrony in a system with identical and linear local population dynamics (Moran 1953). Given the extensive temporal variation observed in the synchrony of weather, we used a simulation model to ask two related questions. First, does temporal variation in environmental synchrony cause changes in population synchrony? Second, because higher, constant levels of population synchrony are known to increase the amplitude of regional population fluctuations, we ask if these short-term changes in population synchrony have an effect on regional (system-wide) population dynamics.

The model system consisted of  $i = 1, 2, \dots, 100$  local populations, each governed by the second order autoregressive (AR2) model

$$x_i(t) = \alpha_1 x_i(t-1) + \alpha_2 x_i(t-2) + \xi_i(t) \quad (1)$$

where  $x_i$  was log-population density of the local populations,  $i$ , and  $t$  is time. The terms  $\alpha_1$  and  $\alpha_2$  were the strength of direct and delayed density dependence, respectively, and represented the effects of endogenous ecological interactions. The stochastic term,  $\xi_i(t)$ , represented exogenous, density-independent disturbance to the system, as weather conditions might impose. Values of  $\xi_i(t)$  were drawn from a multivariate normal

distribution in which each of the 100 individual elements had a mean of zero and standard deviation of one. The correlation among these distributions represented environmental synchrony ( $S_E$ ), which varied through time. Population synchrony ( $S_P$ ) was calculated with the previously described 3-yr moving window correlations.

The well-characterized AR2 model allowed us to produce a variety of population behaviors by varying parameters  $\alpha_1$  and  $\alpha_2$  (Royama 1992, Box et al. 1994) that influence the rate of changes in population synchrony (Bjørnstad et al. 2008). We considered the parameter range  $\alpha_1^2 + 4\alpha_2 \leq 0$  and  $\alpha_2 \geq -1$ , where, in stochastic models, the model produces dampened oscillations towards the equilibrium with an approximate cycle length of

$$2\pi / \cos^{-1} \left( \frac{\alpha_1}{2\sqrt{-\alpha_2}} \right)$$

(Box et al. 1994). The length of population cycles is unimportant to rates of change in population synchrony (Bjørnstad et al. 2008). Therefore, to reduce the parameter space, we fixed the cycle length of  $x_i(t)$  at 6 yr, selected the desired value of  $\alpha_2$ , and varied  $\alpha_1$  accordingly. The variance and periodicity of  $x_i(t)$  increase at an accelerating rate as  $\alpha_2 \rightarrow -1$  (Box et al. 1994). For example, when  $\alpha_1 = \alpha_2 = 0$ , all variance in  $x_i(t)$  comes directly from  $\xi_i(t)$ , and changes in population synchrony occur immediately. When  $0 < \alpha_2 < 0.5$ , the intrinsic dynamics based on previous system states contribute more to the variance of  $x_i(t)$ , and the rate of synchronization decreases, though these time series remain statistically aperiodic (Bjørnstad et al. 2008). As  $\alpha_2$  is decreased further, periodicity and variance increase rapidly until  $\alpha_2 = -1$ , where  $x_i(t)$  exhibits neutrally stable cycles. Throughout this manuscript, we will use  $\alpha_2$  as a proxy for the strength of intrinsic regulation and the variance and periodicity of  $x_i(t)$ .

To mimic the naturally occurring fluctuations in the synchrony of weather, we used a separate AR2 model

$$S_E(t) = \delta_1 S_E(t-1) + \delta_2 S_E(t-2) + \varepsilon(t) \quad (2)$$

that allowed manipulation of the cycle length and the periodicity of oscillations in  $S_E$  as previously described for Eq. 1. Simulation using Eq. 2 produces time series with zero mean and amplitude dependent on parameter values. To control these properties, we calculated  $S_E$  prior to running the population model and then transformed the  $S_E$  time series to have the desired mean and amplitude, defined as one-half of the span containing 95% of values. Also, based on our empirical findings, we used  $0 \leq S_E \leq 1$  so that  $S_E$  could be asynchronous but not anti-synchronous.

To measure the effect of changes in  $S_E$  on  $S_P$ , we used two complementary bivariate extensions of wavelet analysis the cross-wavelet spectrum and wavelet coherence (Grinsted et al. 2004, Cazelles et al. 2007; details in Appendix B). The cross-wavelet spectrum indicates wavelengths at which both time series share wavelet

power, similar to a covariance, and provides the time-frequency-resolved phase difference between the series. Wavelet coherence indicates consistency in phase difference between two time series with values ranging from 0 (independent time series) to 1 (phase-locked time series). Wavelet coherence rises systematically with increasing cycle length (Maraun and Kurths 2004). Tests for statistical significance are not appropriate for simulated data, so to account for this increase we used the coherence between two random normal distributions to indicate an expected level of coherence at each cycle length.

Next, we evaluated the effect of short-term changes in  $S_E$  on the amplitude of fluctuations in regional population size,  $X(t) = \Sigma x_i$ . While deviations from the mean of  $X(t) = 0$  will clearly not always be high given its periodicity under some parameter values, we expected the largest amplitude fluctuations in  $X(t)$  to occur when  $S_E(t)$  is high. To evaluate this hypothesis, we fit linear ordinary least squares (OLS) regressions between  $S_E(t)$  and the absolute value of  $X(t)$ , where a positive slope indicated that deviations in  $X(t)$  increased as  $S_E(t)$  increased. To facilitate comparisons among simulations with different parameter sets, we standardized  $X(t)$  to zero mean and unit variance prior to fitting the regression. Simulations were conducted in Matlab and were run for 1500 years with the first 500 years discarded to reduce the influence of initial conditions.

#### *Gypsy moth study system*

In its invasive North American range, the gypsy moth has exhibited cyclical population fluctuations throughout much of the 20th century, apparently due to delayed density-dependent mortality caused by a gypsy moth specific nucleopolyhedrovirus (Dwyer et al. 2000). However, extended periods of low gypsy moth density are common (Allstadt et al. 2013) and thought to result from high rates of predation by generalist, small mammal predators in low-density gypsy moth populations (Elkinton and Liebhold 1990, Elkinton et al. 1996). Since 1989, the introduced fungal pathogen *Entomophaga maimaiga* has also been a major source of density-independent mortality in North American gypsy moth populations (Hajek 1999), but the density-dependent viral interactions described previously have not been disrupted (Liebhold et al. 2013). Gypsy moth outbreaks are synchronous over distances up to 1000 km (Peltonen et al. 2002, Haynes et al. 2009a). The role of dispersal in gypsy moth population synchrony over these distances is limited, as female moths in North American populations are unable to fly and larvae typically disperse over distances of a few hundred meters (Mason and McManus 1981). Instead, this synchrony is thought to be caused by meteorological disturbances shared among spatially disjunct populations of gypsy moths and their natural enemies (Haynes et al. 2013).

Gypsy moth population dynamics were assessed using annual aerial defoliation surveys of the northeastern

United States from 1975 to 2009, which indicate the presence/absence of defoliation at a 2-km resolution (Liebhold et al. 1997). The proportion of forest area defoliated by gypsy moth larvae is correlated with gypsy moth population density (Williams et al. 1991, Liebhold et al. 1995). We aggregated the 2-km resolution data into  $64 \times 64$  km grid cells and calculated the proportion of the larger grid cell defoliated annually. This spatial scale provided a continuous variable and smoothed spatial error prevalent over smaller distances, while maintaining a large sample of spatially disjunct populations (Haynes et al. 2013). We excluded areas not generally infested with gypsy moth prior to 1975 (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45) to avoid transient dynamics of newly invaded areas (Bjørnstad et al. 2008), leaving 92 grid cells over  $786 \times 896$  km from western Pennsylvania to Maine (Fig. 1 in Haynes et al. [2009a]).

A limitation of these data is that aerial surveys have a detection threshold of  $\sim 30\%$  defoliation (Ciesla 2000) so low-density gypsy moth population dynamics are not captured. When calculating the gypsy moth synchrony time series, one or both cells in an individual pairwise correlation frequently had zero defoliation in all 3 yr of a time window, causing those pairwise correlations to be undefined. Undefined correlations were excluded from synchrony calculations, reducing the sample size of synchrony estimates during some time windows, particularly during the second half of our study period (1995–2009), when levels of defoliation across the region were generally low. Although we conducted our analyses throughout the full study period, we focused interpretation on the period 1975–1995. Prior to analysis, we fifth-root transformed the zero-heavy defoliation data to remove a strong positive skew (Allstadt et al. 2013) and approximate the normal distribution of the Morlet wavelet (Grinsted et al. 2004).

A previous study linked spatial variation in gypsy moth population synchrony to synchrony of monthly totals of precipitation (Haynes et al. 2013), so we evaluated the effect of temporal variation in monthly precipitation on gypsy moth dynamics. We focused on months that coincided with the development of gypsy moth larvae (April–July), because this life stage typically causes defoliation and has the highest mortality within a generation. We obtained precipitation data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994) at a 4-km resolution and aggregated these values into the same  $64 \times 64$  km grid cells used for gypsy moth defoliation. We calculated interannual synchrony of total precipitation for each month (April–July) as in the weather station analyses.

The periodicity of gypsy moth defoliation, gypsy moth population synchrony, and synchrony in monthly precipitation were assessed using wavelet analysis, and we used cross-wavelet spectrum and wavelet coherency analyses to detect temporal associations between these time series. Statistical significance of the wavelet cross-

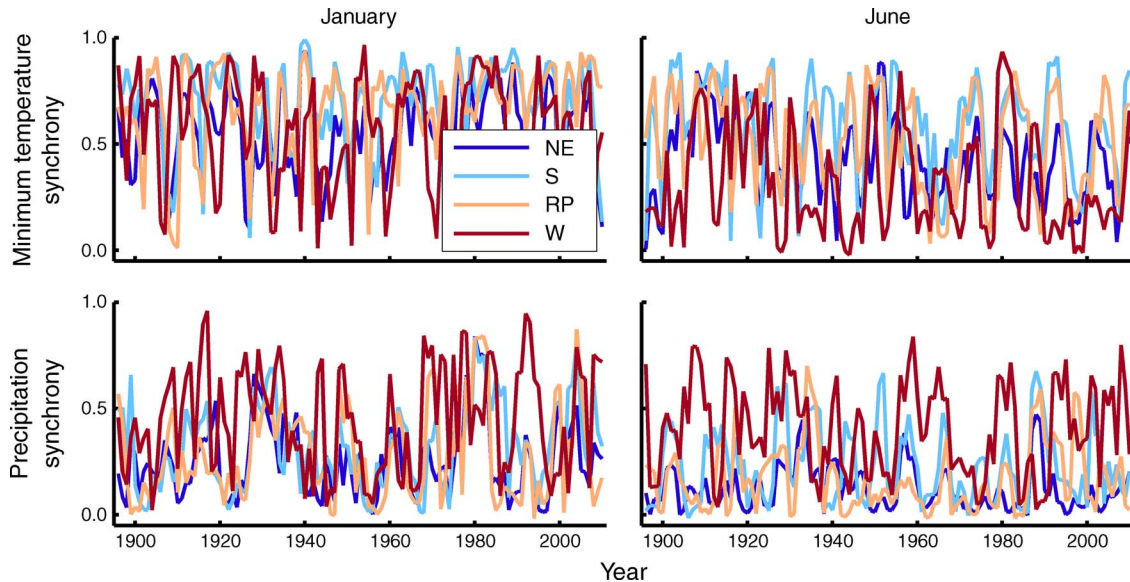


FIG. 1. Time-varying synchrony (top) of mean daily minimum temperature and (bottom) of total precipitation for the months of January and June. Results shown for four of nine climatic regions of the United States designated by the National Climatic Data Center, selected to maximize geographic coverage. Lines indicate the following regions: Northeast (NE), South (S), Rockies and Plains (RP), and the West (W).

spectrum and wavelet coherence were tested using hidden Markov model simulations similar to those described for wavelet analysis (Cazelles et al. 2014).

## RESULTS

### *Temporal patterns in the synchrony of weather*

Patterns of temporal variation in the synchrony of weather varied among weather variables, months, and geographic regions (representative data in Fig. 1; descriptive statistics for all time series in Appendix C). Yearly estimates of synchrony from all time series ranged from  $-0.01$  to  $1$ , and  $<2.5\%$  of readings were negative. Synchrony in minimum and maximum temperatures was generally higher than in precipitation with overall means of  $0.4$ ,  $0.4$ , and  $0.18$ , respectively, though there was considerable variation depending on the month of the year and geographic region. Similarly, the synchrony in temperature displayed higher levels of variation than synchrony in precipitation (Appendix C). Statistically significant periodicity occurred in 186 of the 324 time series, 81, 75, and 78 for minimum temperatures, maximum temperatures, and precipitation, respectively. Of these periodic time series, the cycle lengths ranged from  $\sim 4$  to 32 yr (the longest length that we tested) with a median of 12 yr.

### *Simulation model*

In the simulation model, population synchrony ( $S_P$ ) tracked environmental synchrony under many conditions (Fig. 2a), particularly when local population dynamics were weakly or moderately periodic (Fig. 3). The pattern of temporal variation in  $S_E$  also influenced

the strength of this association. Coherence between  $S_P$  and  $S_E$  was strongest with higher amplitude and more periodic fluctuations in  $S_E$ , while the cycle length (Fig. 3) and the mean level of  $S_E$  (data not shown) had little effect. We also observed phase dependence of  $S_P$  on cycles in regional population density,  $X(t)$ , with higher  $S_P$  during rising and falling phases of the population cycle (Fig. 2a). This is expected when measuring synchrony over time periods shorter than the population cycle length (details in Appendix D). In all cases, the time-invariant synchrony values of  $S_E$  and  $S_P$  were equal. That is, the classic Moran effect still applied.

After establishing that changes in  $S_E$  caused temporal variation in  $S_P$ , we tested our second hypothesis that these short-term changes would alter the amplitude of fluctuations in regional population density. The largest fluctuations in  $X(t)$  occurred when  $S_P$  was high, driven by an increase in  $S_E$  (e.g., years 925–935 in Fig. 2). The effect of  $S_E$  on  $X(t)$  was strongest when local populations were weakly or moderately periodic (Fig. 4). This relationship was also enhanced by increased periodicity of  $S_E$ , whereas reducing the amplitude or cycle length of  $S_E$  reduced the relationship between  $S_E$  and the amplitude of  $X(t)$  (Fig. 4).

### *Case study: the gypsy moth*

Forest defoliation due to gypsy moth larvae was high during the first half of the study period relative to the second half (Fig. 5a). There was a negative trend in the area defoliated from 1975 to 1995, and defoliation was negligible at the regional scale from 1996 to 1999. From 1996 to 1999, 1, 0, 3, and 2 out of 92 grid cells had detectable defoliation, respectively, compared to a

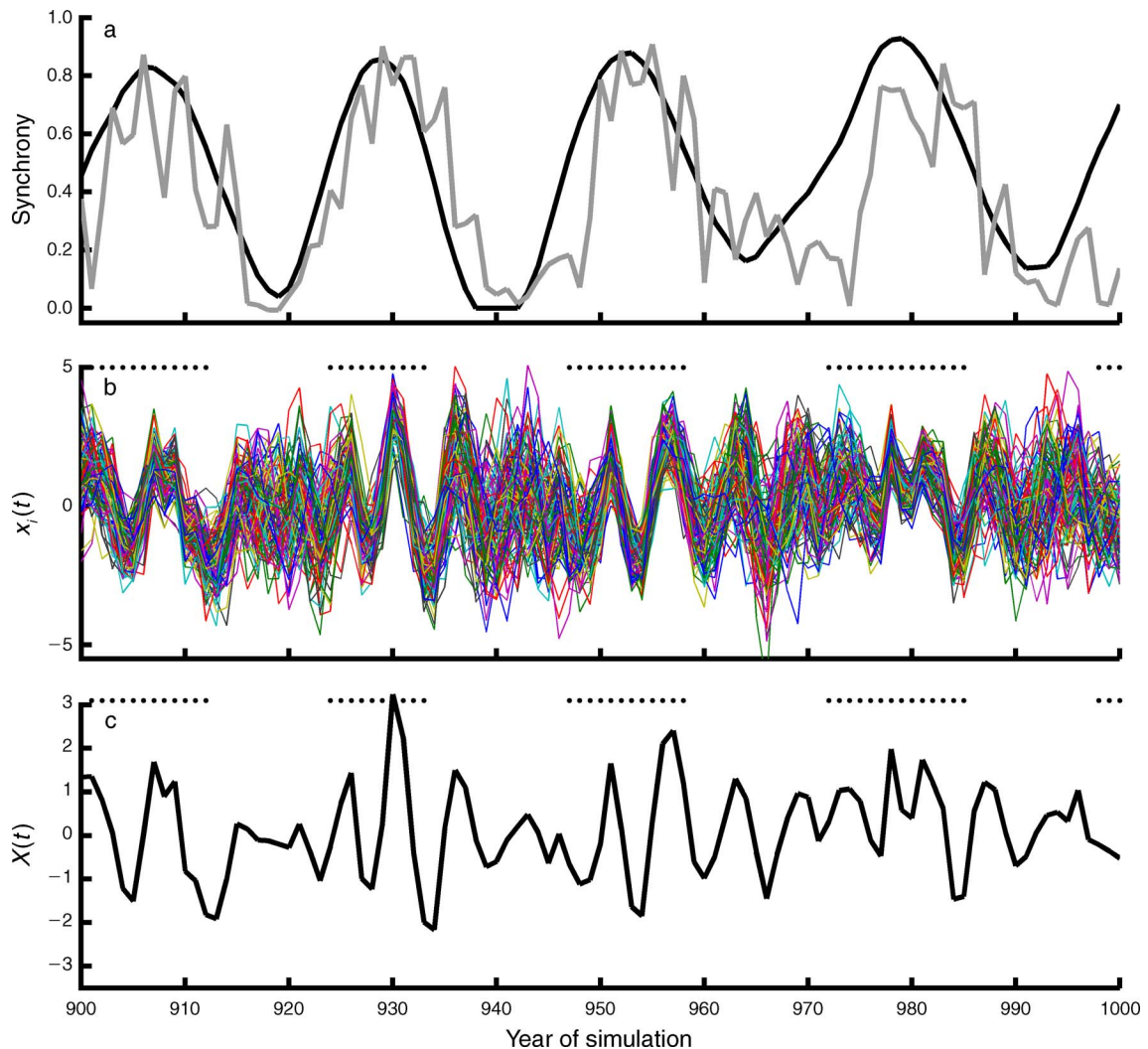


FIG. 2. Sample time series from simulation. (a) Population synchrony ( $S_P$ , gray) generally tracks changes in environmental synchrony ( $S_E$ , black), but see years 990 forward. (b) Local population densities,  $x_i(t)$ , demonstrating changes in  $S_P$  through time,  $t$ , where  $i$  is the population. Black markers (dots above panel) indicate years with  $S_E > 0.5$ . (c) Regional (mean) population density,  $X(t)$ , through time. The largest fluctuations in  $X(t)$  tended to occur when and  $S_P$  and  $S_E$  are high. Markers as in (b). Local population dynamics were moderately periodic ( $\alpha_2 = -0.65$ ; see Eq. 1). Fluctuations in  $S_E$  were highly periodic ( $\delta_2 = -0.95$ ; see Eq. 2) with a cycle length of 24 years, a mean of 0.5, and an amplitude of 0.35. Local population dynamics and variation in  $S_E$  become more periodic as  $\alpha_2$  approaches  $-1$  and  $\delta_2$  approaches  $-1$ , respectively.

maximum of 61 in 1981. The wavelet spectrum of the regional defoliation time series provided evidence that periodic, regional-scale outbreaks occurred from the beginning of the study through the early 1990s at distinct cycle lengths of 4–5 and 8–10 yr (Fig. 5b), though this pattern was not significant for the particular subset of defoliation data used in this analysis. This periodic behavior reflected a pattern of a 4–5 yr cycle in which every other outbreak was larger than those between (Fig. 5a) as observed in earlier studies.

Estimates of gypsy moth population synchrony ranged from 0.04 to 0.98 during our study period. From 1975 to 1995, there were statistically significant 8–10 yr cycles in gypsy moth population synchrony, as well as

nonsignificant evidence for 2–3 yr cycles (Fig. 5c). The 8–10 yr cycles of population synchrony coincide with the 8–10 yr cycles in population density, while the 2–3 yr peaks in population synchrony correspond to the rising and falling phases of 8–10 yr gypsy moth outbreak cycles (Fig. 5a, c).

Spatial synchrony in total June precipitation ( $S_{\text{June}}$ ) fluctuated periodically with a consistent cycle length between 8 and 10 yr (Fig. 5e, f; from 1975 to 1995). The cross-wavelet spectrum showed common power between  $S_{\text{June}}$  and gypsy moth population synchrony at the 8–10 yr cycle length (Fig. 6a), corresponding to the main cycle in  $S_{\text{June}}$  and the double peaks of gypsy moth population synchrony (e.g., 1978–1985 in Fig. 5c). Within this

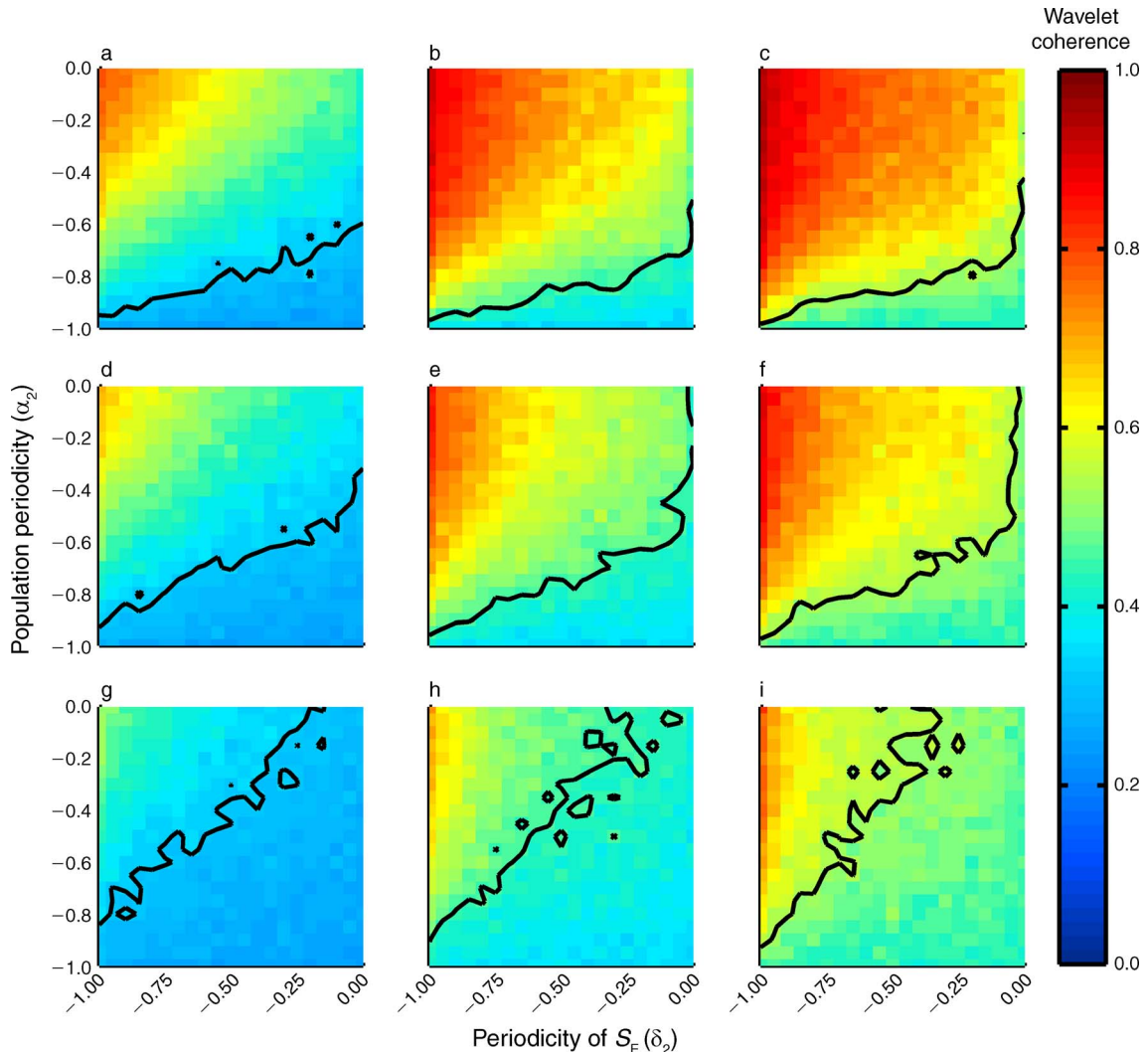


FIG. 3. Wavelet coherence, indicated by color, between  $S_E$  and  $S_P$  from the simulation model, in relation to the periodicity of fluctuations in  $S_E$  and  $S_P$ .  $S_E$  had a mean of 0.5, with amplitude and cycle length as labeled. A coherence of 1 indicates a perfect linear association. Local population dynamics and variation in  $S_E$  become more periodic as  $\alpha_2$  approaches  $-1$  and  $\delta_2$  approaches  $-1$ . Wavelet coherence was measured at the expected cycle length of  $S_E$  and the values shown are the average of 25 simulations. Wavelet coherence increases systematically with the cycle length at which it is measured. As a visual guide, contours contain areas where wavelet coherence was greater than 95% of simulated null series.

region, phase angles between the time series were consistent and near zero. This same area of the spectrum is also significant when standardized into the wavelet coherence (Fig. 6b). We did not find significant areas of wavelet coherence between outbreak synchrony and the synchrony of precipitation in other months that we considered (April, May, and July; Appendix E).

#### DISCUSSION

Whereas many studies have examined changes in population synchrony through space, few have examined temporal variation in population synchrony (Ranta et al. 1998, Forchhammer et al. 2002, Haydon et al. 2003, Post and Forchhammer 2004, Cattadori et al. 2005, Henden et al. 2009). We demonstrate that the

synchrony of weather conditions often varies through time, and our simulation model results indicate that this variation can cause detectable changes in population synchrony under many conditions. Additionally, the resulting temporal variation in population synchrony can alter the amplitude of fluctuations in regional population density. The gypsy moth case study provides suggestive empirical evidence for these theoretical predictions. These results indicate that studying temporal variation in synchrony may provide insights into mechanisms causing population synchrony and increase understanding of population dynamics over large spatial ranges.

The synchrony of weather fluctuated through time in regions throughout the United States. As in ecology,

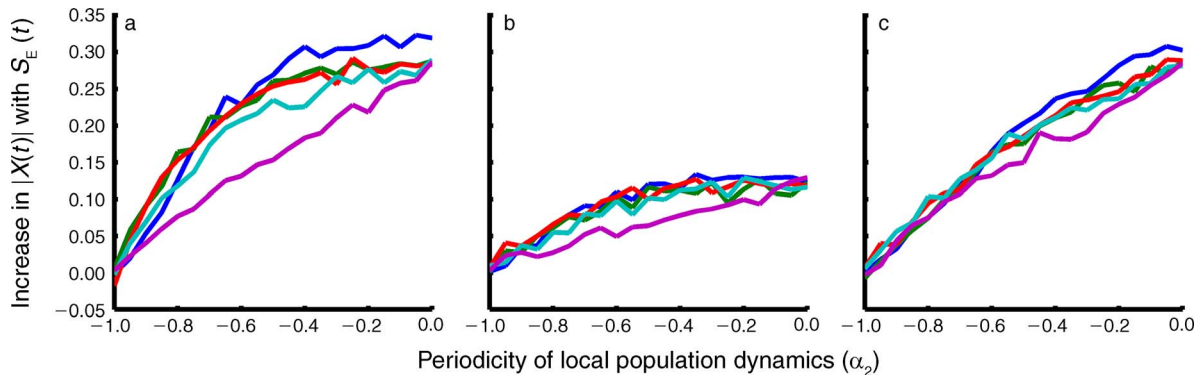


FIG. 4. Regression slopes between the temporary level of environmental synchrony,  $S_E(t)$ , and the amplitude of fluctuations in regional population density,  $|X(t)|$ , for local population dynamics and patterns of periodicity in  $S_E(t)$ . Positive slopes indicate larger variability in  $|X(t)|$  when levels of  $S_E(t)$  are high. Periodicity of  $S_E(t)$  is indicated by line color, with  $\delta_2 = -1, -0.75, -0.5, -0.25$ , and 0 for blue, green, red, teal, and purple. Local population dynamics and  $S_E(t)$  become more periodic as  $\alpha_2$  and  $\delta_2$  approach  $-1$ . Fluctuations in  $S_E(t)$  had amplitude and cycle length of (a) 0.35 and 18 years, (b) 0.15 and 18 years, and (c) 0.35 and 6 years.  $|X(t)|$  was standardized to 0 mean and standard deviation of 1 prior to analysis.

most work in atmospheric sciences on the synchrony of weather conditions (referred to as spatial coherence) has emphasized variation through space rather than through time (Kutzbach 1967, Walsh et al. 1982). In one exception, Haston and Michaelsen (1997) identified changes in synchrony of precipitation over a 400-yr period in southern California, linked to planetary-scale atmospheric circulation patterns (i.e., the El-Niño Southern Oscillation) that alter storm paths through the area. Atmospheric circulation patterns are somewhat periodic (e.g., Wunsch 1999, Frauenfeld et al. 2005) and may cause the statistical periodicity frequently observed in the synchrony of weather, though such an analysis is beyond the scope of this paper. Whether these processes are truly periodic is a matter of debate (e.g., Wunsch 1999). Regardless, our finding that population synchrony will track environmental synchrony through time is general to other forms of variation as well. Periodicity of varying degrees merely provided a convenient way to characterize variability in environmental synchrony in the rest of our study.

In the simulation model, we found that the relationship between temporal variation in environmental synchrony and population synchrony depended on properties of the fluctuations of both environmental synchrony and local population density. Unsurprisingly, effects of environmental synchrony on population synchrony were strongest when fluctuations in environmental synchrony were large in amplitude. Strongly periodic fluctuations in environmental synchrony also enhanced this relationship, representing longer term changes in synchrony to which populations had time to respond. Similarly, highly periodic local population dynamics inhibited the transfer of environmental synchrony to population synchrony because highly periodic populations have a trajectory that is relatively impervious to the influence of environmental stochasticity over the short timescales we are examining (Bjørnstad et al.

2008). However, even among species known for their periodic population dynamics, few if any reach the highest levels of population periodicity considered in our simulation model (Kendall 1998, Liebhold and Kamata 2000). Because weak to moderate periodicity is common in natural populations, temporal changes in the synchrony of weather may drive changes in the population synchrony of a wide range of ecological systems. In these systems, this variation in the strength of the Moran effect provides another method of verifying that population synchrony is caused by environmental synchrony.

The gypsy moth case study provides empirical evidence of temporal variation in the synchrony of weather driving fluctuations in population synchrony, as might be expected given the regular oscillations in the synchrony of June precipitation and weakly periodic gypsy moth population dynamics (Liebhold et al. 2000). The case study also demonstrates that the linkage between population and environmental synchrony phenomenon can be useful in identifying potential mechanisms causing population synchrony, particularly in systems with limited dispersal. Previous work linked synchrony in precipitation totals from all months with geographic variation in the synchrony of gypsy moth outbreaks (Haynes et al. 2013). We have apparently narrowed down the synchronizing effect to total June precipitation, at least during periods of widespread gypsy moth outbreaks. The mechanism through which precipitation synchronizes gypsy moth populations remains unclear. Weather may synchronize gypsy moth populations directly through effects on mortality or survivorship, or indirectly such as through effects on oak masting and predators of the gypsy moth that depend on acorns for winter survival (Haynes et al. 2009a, 2013).

In our model, as in Moran (1953) and Bjørnstad et al. (2008), local population dynamics are governed by a

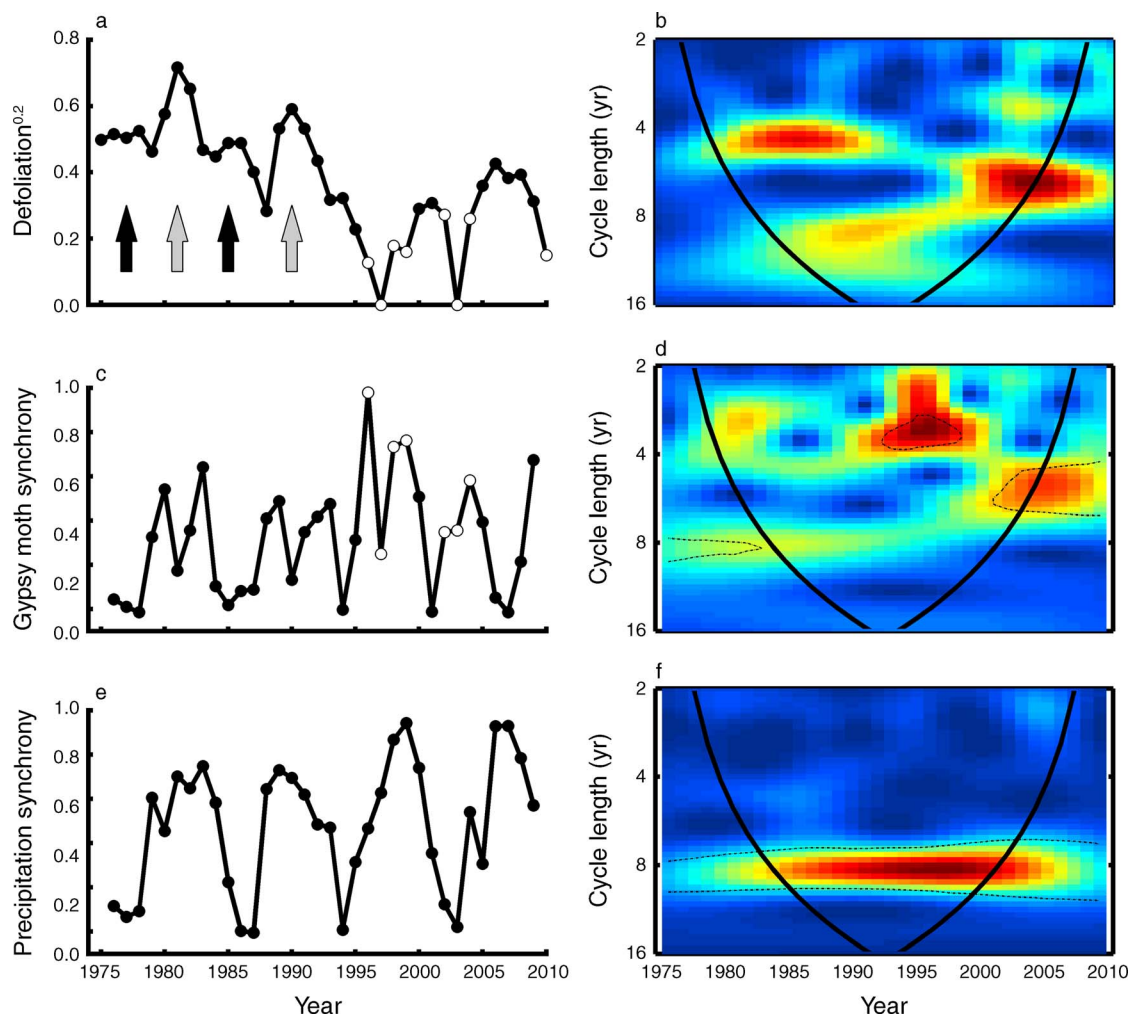


FIG. 5. Time series of (a) regional defoliation by gypsy moths, (c) gypsy moth population synchrony, (e) synchrony of total June precipitation, and (b, d, f) corresponding wavelet spectra. (a) Defoliation totals were fifth-root transformed and then standardized to zero mean and unit variance. Peaks in the 4–5 and 8–10 year cycles are indicated by black and gray arrows, respectively. Open circles indicate years with defoliation in fewer than 10 grid cells. (b, d, f) Red areas within the wavelet spectrum indicate higher power (evidence for periodicity); blue areas denote lower power. Dashed lines contain regions of statistically significant periodicity. Below the thick curved lines, power values are subject to edge effects and must be interpreted with care.

constant second-order autoregressive model with no dispersal among populations. High levels of dispersal may dampen temporal variability in population synchrony (Ranta et al. 1998), and shifts in local population dynamics can also cause changes in synchrony through time (Henden et al. 2009). Additionally, nonlinear population dynamics (Ranta et al. 1997, Engen and Sæther 2005) and spatial heterogeneity (Peltonen et al. 2002, Engen and Sæther 2005, Liebhold et al. 2006) affect overall levels of synchrony and the decay of synchrony through space, but it is less clear how they would affect variation through time. More theoretical work is needed to determine if the impacts of temporal variation in synchrony are maintained in more complex models. However, empirical results from the gypsy moth case study suggest that temporal variation in environ-

mental stochasticity can influence the synchrony of populations governed by nonlinear trophic interactions (Dwyer et al. 2004, Allstadt et al. 2013).

Consistently high levels of population synchrony are known to promote large, regional-scale fluctuations in population densities that can increase the risk of rare species extinction or widespread outbreaks of pest species (Heino et al. 1997, Liebhold et al. 2012). Our results indicate that short-term variation in population synchrony, caused by changes in environmental synchrony, can also influence the amplitude of regional density fluctuations. This finding offers an explanation for observed dynamic patterns of regional gypsy moth outbreaks, in which each large outbreak (occurring at 8–10 year intervals) tends to be followed by a smaller outbreak 4–5 years later (Fig. 5a; Johnson et al. 2006,

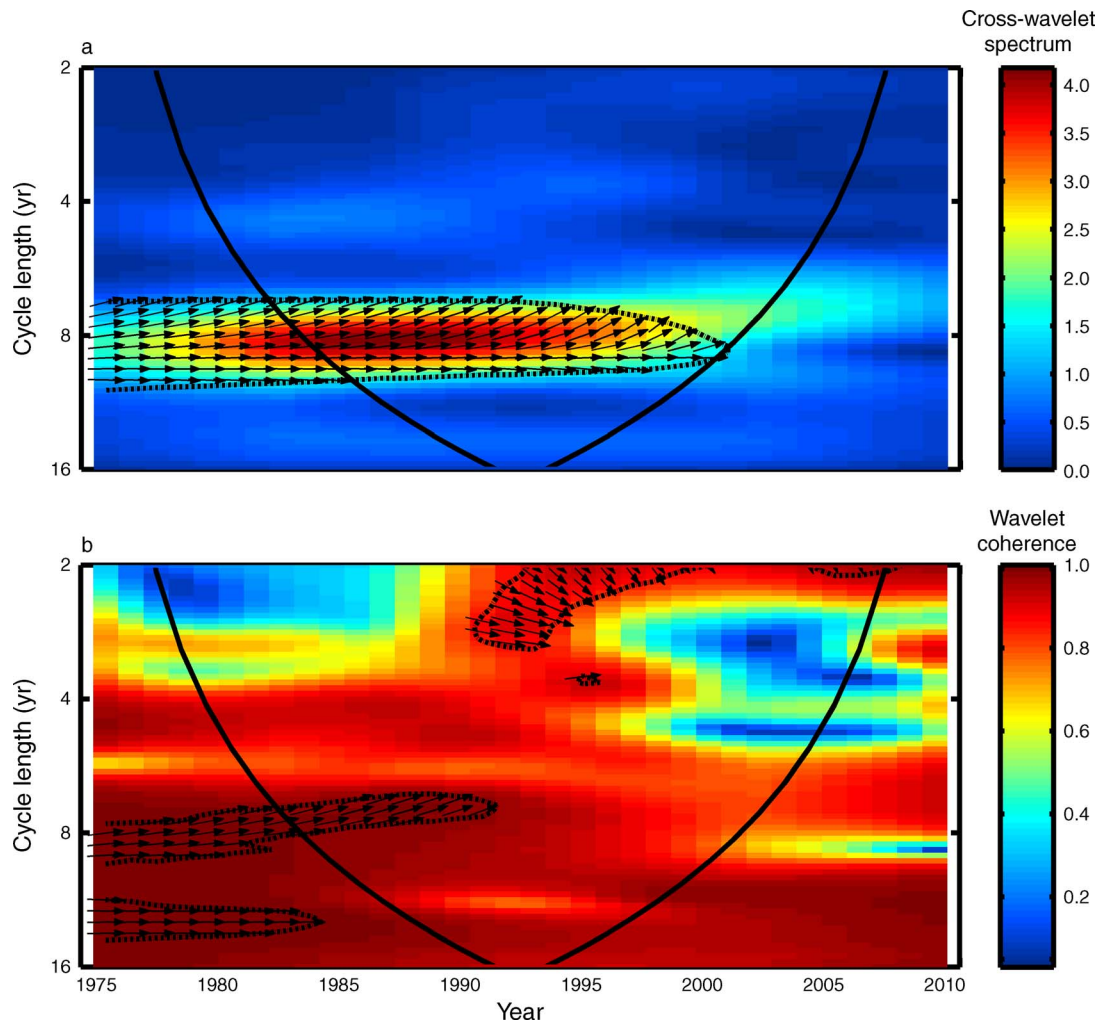


FIG. 6. The (a) cross-wavelet spectrum and (b) wavelet coherence between gypsy moth population synchrony and synchrony of total June precipitation. Dashed lines indicate areas of the spectra that are statistically significant. Arrows indicate the phase difference between the two time series, where a right-facing arrow indicates that the time series are in phase and a left-facing arrow means that the series are in anti-phase. Arrows pointing up indicate that synchrony of June precipitation led synchrony of defoliation by a fraction of a cycle length.

Haynes et al. 2009b). Previous theoretical work has hypothesized that these smaller outbreaks may be caused by inter- or intraspecific interactions, such as dispersal among areas with variable predation pressure (Bjørnstad et al. 2010) or induced defenses of the host trees (Elder et al. 2013). However, our results indicate that this pattern may instead be a consequence of temporal variation in the synchrony of weather, as the larger outbreaks occurred when the synchrony of weather, and therefore population synchrony, was high and the smaller outbreaks occurred when the synchrony of weather was low. This suggests that monitoring for unusually synchronous weather conditions might provide early warning of unusually widespread pest outbreaks. Temporal variation in environmental and population synchrony may also be relevant to the conservation of rare species because in current popula-

tion viability analyses, the degree of population synchrony is typically assumed to be constant through time (e.g., Akçakaya and Root 2002), thereby ignoring the possibility of recurring periods of high population synchrony and potentially underestimating extinction risk.

The findings presented here suggest a new role of weather in the cyclical population dynamics of many animals. Early studies indicated that dynamics of insects and small mammals may be primarily driven by, or indeed track, temporal variation in meteorological conditions (e.g., Elton 1924, Davidson and Andrewartha 1948). However, more rigorous searches have failed to yield evidence for population density tracking meteorological conditions (Martinat et al. 1987, Elkinton and Liebhold 1990). Though meteorological cycles influence populations in a variety of ways (Stenseth et al.

2003), population cycles are now generally thought to arise from trophic interactions (Berryman 1996, Stenseth 1999, Myers and Cory 2013), whereas the primary observed role of weather is synchronization of dynamics (Moran 1953, Royama 1992). The results presented here provide new evidence for the importance of meteorological conditions to regional population dynamics. Specifically, we have learned that while population cycles may not be directly driven by meteorological cycles, changes in the synchrony of weather might be an important driver of the amplitude of animal population oscillations at regional scales.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-1497.1.sm>