



IDEA AND PERSPECTIVE

The geography of spatial synchrony

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Abstract

Spatial synchrony, defined as correlated temporal fluctuations among populations, is a fundamental feature of population dynamics, but many aspects of synchrony remain poorly understood. Few studies have examined detailed geographical patterns of synchrony; instead most focus on how synchrony declines with increasing linear distance between locations, making the simplifying assumption that distance decay is isotropic. By synthesising and extending prior work, we show how *geography of synchrony*, a term which we use to refer to detailed spatial variation in patterns of synchrony, can be leveraged to understand ecological processes including identification of drivers of synchrony, a long-standing challenge. We focus on three main objectives: (1) showing conceptually and theoretically four mechanisms that can generate geographies of synchrony; (2) documenting complex and pronounced geographies of synchrony in two important study systems; and (3) demonstrating a variety of methods capable of revealing the geography of synchrony and, through it, underlying organism ecology. For example, we introduce a new type of network, the synchrony network, the structure of which provides ecological insight. By documenting the importance of geographies of synchrony, advancing conceptual frameworks, and demonstrating powerful methods, we aim to help elevate the geography of synchrony into a mainstream area of study and application.

Keywords

Graph theory, gypsy moth, *Lymantria dispar*, modularity, spatial synchrony, synchrony network, terrestrial primary productivity.

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INTRODUCTION

Spatial synchrony, defined as correlated fluctuations among spatially disjunct populations, is a fundamental aspect of population dynamics (Liebhold *et al.* 2004) that has long intrigued ecologists (Elton & Nicholson 1942; Moran 1953), resulting in an extensive literature documenting synchrony in diverse taxa such as plankton (Vasseur & Gaedke 2007; Defriez *et al.* 2016), insects (Hanski & Woiwod 1993), birds (Koenig & Liebhold 2016) and many others (Liebhold *et al.* 2004). Synchrony is ubiquitous, and occurs at distances up to thousands of kilometres (Post & Forchhammer 2002; Koenig & Liebhold 2016). Some practical implications of synchrony are well known, e.g. metapopulations are at greater risk of overall extinction if component populations are synchronously rare (Heino *et al.* 1997; Earn *et al.* 2000), while the synchrony of pest outbreaks exacerbates ecological and socioeconomic impacts (Liebhold *et al.* 2012). Recent work posits that spatial synchrony has implications for community dynamics and ecosystem function (Defriez *et al.* 2016).

Despite its importance in ecology, many aspects of synchrony are still poorly understood. Difficulties have arisen in determining which mechanism, or combination of mechanisms, causes synchrony. Synchrony is thought, generally, to arise from three mechanisms, alone or in combination: dispersal between populations; Moran effects, i.e. the synchronising influence of correlated fluctuations in environmental drivers of population dynamics (Moran 1953); and trophic interactions with synchronised or mobile species (Liebhold *et al.* 2004). However, using the most common past approaches, statistical patterns of synchrony resulting from each of these mechanisms can be similar (Ranta *et al.* 1999; Kendall *et al.* 2000; Abbott 2007). It is the specific combination of causes that pertains in a situation, and their relative importance, that has seldom been determined, except in special cases where certain drivers are known to be absent (e.g. if landscape structure prevents dispersal; Grenfell *et al.* 1998).

Recently, spectral approaches for studying synchrony have grown in popularity (Viboud *et al.* 2006; Vasseur & Gaedke 2007; Keitt 2008; Sheppard *et al.* 2015). These approaches allow the decomposition of synchrony according to the

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timescales at which it occurs, and can help identify causes of synchrony (Sheppard *et al.* 2015); but they are still uncommonly applied, have limitations, and have also led to new questions that highlight our ignorance about synchrony. Recent studies using spectral and other methods have documented changes in synchrony over time, some of which were abrupt, were possibly caused by climate change, and were ecologically or economically consequential (Post & Forchhammer 2004; Allstadt *et al.* 2015; Sheppard *et al.* 2015; Defriez *et al.* 2016; Koenig & Liebhold 2016; Shestakova *et al.* 2016). These studies beg the question of whether synchrony commonly changes in intensity or structure, and if so, why (Sheppard *et al.* 2015)? It is possible that changes in synchrony are another manifestation of climate change. This is an important consideration but is as yet poorly documented (Post & Forchhammer 2004; Sheppard *et al.* 2015; Koenig & Liebhold 2016; Shestakova *et al.* 2016).

Spatial dimensions of synchrony are still rarely explored in detail in ecology. Historically, the most common approaches for studying population synchrony emphasised the relationship between synchrony and the distance between sampling locations (Bjørnstad *et al.* 1999; Bjørnstad & Falck 2001). While this is technically a spatially oriented approach, it makes the simplifying choice to treat patterns of synchrony as one-dimensional even though geographical space is at least two-dimensional. Only if the landscape is homogenous and the pattern of change in mechanisms of synchrony is isotropic would this be an adequate assumption. Thus, the simplification probably limits past statistical descriptions of synchrony by obscuring information that may help reveal causes, changes and important consequences of synchrony.

Relatively few studies have exploited detailed spatial aspects of synchrony to more fully reveal ecological processes (e.g. Bellamy *et al.* 2003; Haynes *et al.* 2009b, 2013; Gouveia *et al.* 2016). Gouveia *et al.* (2016) developed extensions of the non-parametric covariance function (Bjørnstad & Falck 2001) and the partial Mantel correlogram (Bjørnstad *et al.* 1995) that calculate synchrony as a function of distance while accounting for a second covariate. Haynes *et al.* (2013) depicted spatial synchrony in gypsy moth outbreaks in detail as a matrix of pairwise correlations between locations and used matrix regression to investigate the importance of potentially synchronising factors. Defriez & Reuman (*in press a*) mapped spatial variation in vegetation synchrony and inferred causes of synchrony from its spatial variation. These and other studies (Bjørnstad & Bascompte 2001; Powney *et al.* 2012; Mortelitti *et al.* 2015) indicate the importance of spatial patterns beyond distance decay, but there are few such studies and we argue that they should be the tip of the iceberg: opportunities greatly eclipse what has been accomplished so far.

Here, we study the ‘geography of synchrony’ by synthesising and extending past spatial work on synchrony. We demonstrate that the geography of synchrony is worthy of study in its own right as a major phenomenon that relates to many areas of ecology. We argue that studies of the geography of synchrony can produce advances on important applied and pure-science questions. We describe ways that the geography of synchrony can illuminate mechanisms of synchrony, changes in synchrony, and the relationship between synchrony

and the ecology of an important model species. Benefits of a spatial approach to synchrony in epidemiology have already been great, revealing important aspects of the transmission dynamics of major diseases such as measles (Grenfell *et al.* 2001; Jandarov *et al.* 2014), influenza (Viboud *et al.* 2006), dengue (Cummins *et al.* 2004) and rotavirus (Pitzer *et al.* 2009). We argue that benefits to ecology can be at least as great.

In the second section, we categorise theoretical mechanisms that can generate geographies of synchrony; in the third section, we apply these ideas showing that causes of synchrony can be inferred from the geography of synchrony. In the fourth section, we use satellite data to illustrate that the synchrony of peak-growing-season normalised difference vegetation index (NDVI) values across the United States has a pronounced geography; in the fifth section, we demonstrate that geography of synchrony must be one of the key aspects considered in future studies of possible shifts in synchrony through time, and their consequences and causes. In the sixth section, we introduce new network-based methods of studying the geography of synchrony; in the seventh section, we demonstrate how these tools can be applied to illuminate the ecology of the gypsy moth, a classic model species for spatiotemporal population dynamics studies. The eighth section is the Discussion.

MECHANISMS OF GEOGRAPHY OF SYNCHRONY

Population synchrony may exhibit spatial structure for at least four reasons. First, (A) there may be geographical patterns in the synchronising driver itself, i.e. the driver may be more correlated between some pairs of locations than others. For example, if populations are distributed on either side of a mountain range, and an environmental driver is synchronised on both sides of the range, but not across it, populations may be synchronised similarly. Traditional approaches plotting the dependence of synchrony on distance between sampling sites will suggest that synchrony is weak overall, obscuring the strongly synchronised groups on either side of the mountain range. This is a simplified illustration: real habitat structure may be complex, with cryptic geographical divisions between subgroups. Second, (B) density-dependent population regulation may differ among locations, so that the way environmental fluctuations drive dynamics varies spatially (Liebhold *et al.* 2006; Bjørnstad *et al.* 2010). Variation in density dependence may result from heterogeneity in environmental quality or from complex interactions including differences in effects of natural enemies (Hanski *et al.* 1991). Sites with different density-dependent dynamics are expected typically to show reduced synchrony, so spatial variation in density dependence can produce geography of synchrony (Hugueny 2006). Third, (C) limiting factors for population growth may vary spatially, causing spatial shifts in which environmental factor drives dynamics. This may be particularly important along latitudinal or elevational gradients, as temperature (for instance) may more strongly influence population fluctuations nearer to a species’ climatic niche boundary. Finally, (D) dispersal among populations may be unequal due to physical barriers and landscape structure. Effects of landscape structure on

connectivity and movement rates are well documented (Tischendorf & Fahrig 2000). Populations more connected by dispersal should be more synchronous. The four mechanisms may operate alone or in combination, or populations may be affected by multiple instances of one mechanism, e.g. there may be two synchronising environmental variables, each with its own spatial structure.

Mechanisms A–D are not mechanisms of synchrony, *per se*, but rather are mechanisms by which synchrony can vary spatially. A and D relate to mechanisms of synchrony in that they reflect spatial structure in Moran effects and dispersal, which are mechanisms of synchrony. On the other hand, B produces geography of synchrony by altering synchrony which arose by Moran effects or dispersal or another mechanism, in a spatially variable way.

To demonstrate that mechanisms A–D can, indeed, produce geography of synchrony, we simulated them using a vector autoregressive moving average model, which is a linearisation of a very general model (see Appendix S1 in Supporting Information) that can encompass a variety of common modelling frameworks. Our model considers populations at locations $i = 1, \dots, P$, which are linked by dispersal and influenced by spatially correlated environmental fluctuations (Moran effects). Deviation of the population in patch i from the within-patch carrying capacity is denoted $w_i(t)$ for time t . Environmental conditions for potential drivers are denoted $\varepsilon_i^{(j)}(t)$. Dispersal is implemented via a $P \times P$ matrix, D . The model is:

$$\begin{pmatrix} w_1(t) \\ \vdots \\ w_P(t) \end{pmatrix} = D \begin{pmatrix} \sum_{l=1}^a m_{1l} w_1(t-l) + \sum_{j=1}^b \sum_{l=0}^c q_{1l}^{(j)} \varepsilon_1^{(j)}(t-l) \\ \vdots \\ \sum_{l=1}^a m_{Pl} w_P(t-l) + \sum_{j=1}^b \sum_{l=0}^c q_{Pl}^{(j)} \varepsilon_P^{(j)}(t-l) \end{pmatrix}. \quad (1)$$

The autoregressive coefficients m_{il} control density dependence in habitat patch i , and the moving average coefficients $q_{il}^{(j)}$ control the influence of the environmental variables. The parameters a , b and c denote the numbers of autoregressive lags, environmental drivers and moving average lags respectively. Spatial structures in environmental fluctuations $\varepsilon_i^{(j)}(t)$ are controlled by $P \times P$ covariance matrices Ω_j . For present purposes, environmental fluctuations are assumed to be independent of each other and through time, and Gaussian with mean 0 and variance 1 within each patch (i.e. diagonal entries of the Ω_j are 1). We considered $b = 3$ environmental drivers, the first two representing regionally correlated fluctuations (i.e. for $j = 1, 2$, Ω_j had positive off-diagonal entries), and the third representing local (spatially uncorrelated) environmental noise. This model can implement any combination of mechanisms A–D.

We here describe, in general terms (Appendix S2 has details), example simulations corresponding to each mechanism acting in isolation. We used each mechanism to generate $P = 16$ population time series. Each mechanism was implemented following a spatial structure consisting of two disjoint eight-location sets, S_1 and S_2 , among the 16 generated, so that if the mechanism generates a geography of population synchrony it should reflect that structure. To implement

mechanism A (spatial patterns in a synchronising driver), we specified the covariance matrix Ω_1 of the synchronising environmental driver $\varepsilon_i^{(1)}(t)$ to vary in the off-diagonal as a block matrix: entries controlling environmental covariance between locations within S_1 (respectively, within S_2) were large (0.6), and those controlling environmental covariance between locations in different sets were small (0.3). To implement mechanism B (differences in density dependence), we altered the m_{il} such that all locations were governed by autoregressive order 2 (AR(2)) dynamics generating periodic oscillations under stochastic excitation, but each set of locations had different parameters, yielding periodicities of ≈ 5 time steps for S_1 and ≈ 16 time steps for S_2 . To implement mechanism C (spatial changes in the operating environmental driver), we manipulated the $q_{il}^{(j)}$ such that populations in S_1 and S_2 were sensitive to different drivers, $\varepsilon_i^{(1)}(t)$ and $\varepsilon_i^{(2)}(t)$ respectively. To implement mechanism D (structured dispersal), we altered the dispersal matrix D so that 40% of individuals from each location in S_1 dispersed equally to other locations in S_1 , but not to S_2 ; and, respectively, for S_2 . Parameters unrelated to the operating mechanism were spatially homogeneous (Appendix S2).

Possible geographies of synchrony produced by our model were represented as matrices of Pearson correlation coefficients between simulated population time series in location pairs (16×16 matrices). Location membership in each set differed for the different simulations, i.e. S_1 and S_2 were chosen differently for each mechanism, so that geographical signatures of the different mechanisms could be distinguished. However, other than aiding in visual interpretation of results, these distinctions are arbitrary, since location numbers are arbitrary in our setup. For mechanism A, S_1 was $\{1, \dots, 8\}$; for B, it was $\{1, \dots, 4, 9, \dots, 12\}$; for C, it was $\{1, \dots, 4, 13, \dots, 16\}$; for D, it was $\{1, 2, 5, 6, 9, 10, 13, 14\}$.

Results indicated that each mechanism can indeed produce a geography of synchrony. Structure corresponding to S_1 and S_2 was present in each population correlation matrix (Fig. 1). Correlation matrices are accompanied in Fig. 1 by representations of the spatial structure S_1 and S_2 . In each case, there is a visual match, suggesting that geography of synchrony may be a powerful diagnostic tool in the inference of causes of synchrony and variation therein in real data. This possibility is further explored in the next section.

APPLICATION: INFERENCE OF THE CAUSES OF SYNCHRONY

As Fig. 1 suggests, geography of synchrony can be an important new tool for inferring mechanisms of synchrony. A few prior studies have used this tool. For instance, Defriez and Reuman mapped global spatial variation in synchrony of marine chlorophyll *a* (Defriez & Reuman *in press b*) and terrestrial vegetation (Defriez & Reuman *in press a*), and used spatial statistics to infer causes of synchrony from the spatial patterns obtained. This map-based approach is discussed in more detail in the fourth section.

Inferences have also been performed using matrix regression (Legendre *et al.* 1994; Lichstein 2007). Matrix regressions extend the widely used Mantel test (Mantel 1967) by assessing

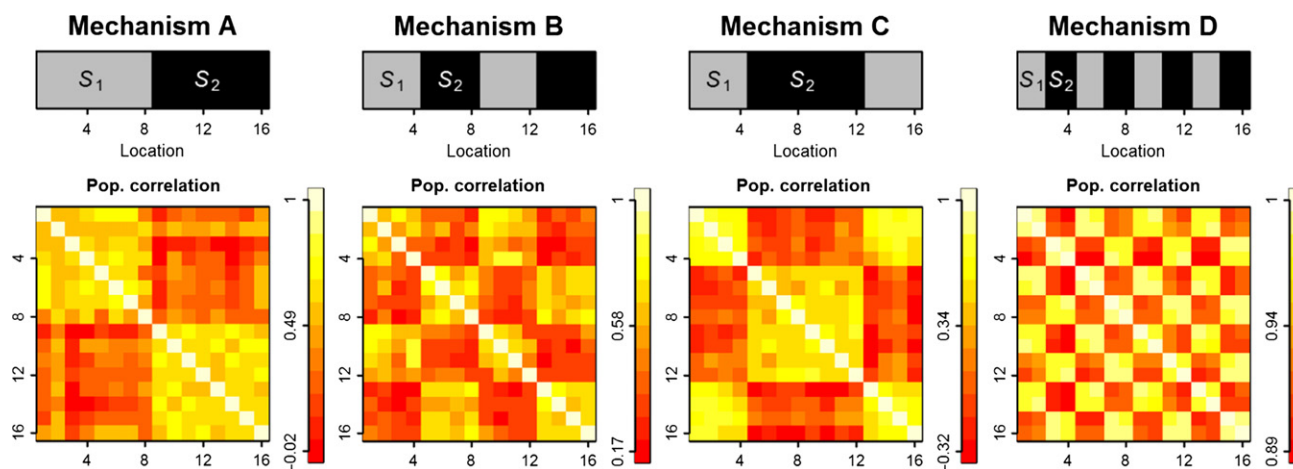


Figure 1 Illustrations of geography of synchrony caused by mechanisms A–D. Top panels depict spatial structures built into a model (eqn 1) using: mechanism (A) spatial pattern in the synchrony of an environmental driver; mechanism (B) differences in density dependence; mechanism (C) differences in sensitivity to drivers; mechanism (D) unequal dispersal rates. Bottom panels demonstrate that the population correlation matrix from each simulation shows geography of synchrony reflecting mechanism spatial structure. See text for details.

the relationship between a response matrix and multiple predictor matrices, each consisting of pairwise similarities (or differences) between locations. The approach exploits the geography of synchrony because it examines whether pairs of locations which are more similar with respect to some geographical predictor(s) are also significantly more synchronous. Haynes *et al.* (2013) argued using this approach that synchrony in spring precipitation caused, in part, synchrony in gypsy moth defoliation.

We argue below that matrix regressions are a potentially useful but underexploited tool for inferring causes of synchrony from geographical patterns. We also elaborate on matrix regression, providing novel model selection tools. Because synchrony is a type of similarity, and to simplify interpretation of results, we consistently use similarity matrices in statistical models, but using dissimilarity matrices (or some of each) is also valid (Legendre & Legendre 1998).

We analysed our simulated data to test whether matrix regression can uncover the mechanisms that underlie each simulation. In addition to mechanisms A–D described above, we created a fifth scenario that combined multiple mechanisms for a stronger test of the matrix regression methods. The combined scenario included two Moran driver variables, $\varepsilon_i^{(1)}(t)$ and $\varepsilon_i^{(2)}(t)$, having different spatial structures, with populations equally sensitive to both, as well as spatially structured dispersal (Appendix S2 has details). Response matrices in matrix regressions were the population correlation matrices (e.g., Fig. 1a–d). Predictor matrices represented mechanisms A–D. Representing mechanism A (spatial patterns in driver synchrony) were correlation matrices for the stochastic realisations of $\varepsilon_i^{(1)}(t)$ and $\varepsilon_i^{(2)}(t)$ that occurred in the simulations. For B (changes in density dependence), we measured pairwise similarities in density dependence between locations. Similarities were measured by first fitting AR(2) processes separately to the simulated data from the two locations, and then analytically calculating the expected correlation between the fitted processes if they were stimulated by identical white noise. This

is the reduction from the Moran expectation of perfect population correlation that would occur if AR coefficients were the same (Moran 1953; Appendix S3 for mathematical details). Mechanism C (changing sensitivity to drivers) was quantified by first measuring driver sensitivities using wavelet coherences (Sheppard *et al.* 2012) between simulated population i and realisations of the environmental drivers $\varepsilon_i^{(1)}(t)$ and $\varepsilon_i^{(2)}(t)$, for all locations i . This gives, for each location, two vectors of coherences indexed by timescale. Differences between sites in these coherence vectors were computed based on the L^2 norm and were then transformed to between-site similarity values. Mechanism D (differences in dispersal rate) was represented using the dispersal matrix D from model setup.

In linear regression and other contexts, model selection based on information criteria (such as the Akaike Information Criterion, AIC) is frequently performed to identify which biological mechanism(s) are best supported by data (Burnham & Anderson 2002; Clark & Gelfand 2006). Because matrix modelling uses a resampling framework instead of likelihood, standard model selection is unavailable. We developed analogous tools, based on leave- n -out cross validation and resampling, that make it possible to perform model selection on matrix models. The tools yield *model rankings* and, importantly, *model weights*, which sum to 1 across the models considered and which can be interpreted as the relative support for each model. Briefly, we rank models by iteratively leaving out n sites at random and using these n sites for out-of-sample predictions from each of our candidate models; the best model has the lowest out-of-sample error rate. We then resample locations many times and rank models for the resampled data sets, using the fraction of times a candidate model is the top model as its weight (see Appendices S4 for mathematical details and S10 for R code). By summing model weights across models containing a predictor, one can generate a *predictor importance weight* for each predictor. We generated these weights for each simulated dataset. This approach has the same advantages over standard hypothesis testing that

AIC-based model selection has over stepwise methods in multiple linear regression (Burnham & Anderson 2002). A likelihood-based approach to matrix regression has been applied in genetics (Yang 2004; Peterman *et al.* 2014), but that approach does not apply to studies of synchrony because the statistical model used does not preserve positive semidefiniteness, an inherent property of population correlation matrices.

Matrix regression and model selection accurately discriminated drivers of synchrony and mechanisms underlying its geography in simulated data, building confidence in the techniques (Table 1). Across all four single-mechanism simulations, the main operating mechanism was identified as a significant determinant of the geography of synchrony, and received large predictor importance weight. Model selection results paralleled standard permutation-based hypothesis tests for matrix regression, supporting our model selection approach. As with mechanisms A–D in isolation, when we combined mechanisms to create a stronger test, matrix regression identified the operating mechanisms (Table 1).

In two cases (mechanisms B and D in Table 1), a geography of synchrony of environmental drivers arose only through sampling variation, but nevertheless the driver synchrony matrix was a significant predictor of the population synchrony matrix, indicating that matrix regression can very sensitively infer environmental drivers of synchrony. For these simulations, the off-diagonals of Ω_1 and Ω_2 contained a non-zero constant, but of course a correlation matrix of simulated environmental time series would have some random variation in its off-diagonal. In empirical cases, inference from subtle geographical patterns will be complicated by factors including measurement error and collinear environmental variables. Additionally, substantial population dynamic non-linearities can affect synchrony and may hinder inferences made via linear approaches such as ours, for instance, because of emergence of complex self-organised spatiotemporal patterns such as travelling waves, non-linear phase-locking or spatial chaos

(Hassell *et al.* 1991; Sole *et al.* 1992; Bjørnstad 2000; Bjørnstad & Bascompte 2001).

In the above matrix modelling exercises, predictor and response matrices were constructed from simulated data in all cases except for the dispersal matrix, D , which was used directly. This represents what could be done in an application of matrix modelling to real data, in which case population and environmental time series may be available but the nature and parameterisation of dynamics would be unknown. Although D would typically not be available, it can sometimes be hypothesised from information on habitat structure and knowledge of species biology (Bellamy *et al.* 2003; Powney *et al.* 2012; T L Anderson *et al.* unpublished data).

MAPPING SPATIAL VARIATION IN SYNCHRONY

Geographies of synchrony can be mapped to characterise spatial variation in the degree of regional or local spatial synchrony. A recent approach measures synchrony in neighbourhoods defined by a moving window. For each location, some metric of average synchrony among nearby locations is computed; these values are then mapped (Defriez & Reuman *in press a,b*). We apply this method to 1989–1998 time series of annual peak terrestrial vegetation greenness (NDVI) derived from Advanced Very High Resolution Radiometer (AVHRR) satellite imagery for the contiguous USA (Fig. 2a). Data are at $1 \times 1 \text{ km}^2$ resolution, and synchrony for each grid cell was quantified as the mean Pearson correlation (over time) between the cell and others within 10 km. Because of its analogies in geostatistics (e.g. Anselin 1995), Gouveia *et al.* (2016) coined this approach ‘non-centered local indicators of spatial association’ (nCLISA). Data processing is explained in Appendix S5.

Pronounced geography of synchrony is apparent in the NDVI data (Fig. 2a). The wide variation in synchrony, spanning essentially the entire typical range of the statistic (0–1),

Table 1 Matrix regression recovers operating mechanisms A–D of geography of synchrony in simulated data, and in a complex scenario with combined mechanisms. Bold font indicates statistically significant effects.

Simulated scenario	Driver 1 synchrony	Driver 2 synchrony	Density dependence	Driver sensitivity	Dispersal
A) Driver 1 synchrony pattern	$\beta = \mathbf{0.944}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{1.000}$	$\beta = 0.037$ $P = 0.477$ $\Sigma w = 0.095$	$\beta = -0.122$ $P = 0.627$ $\Sigma w = 0.225$	$\beta = 0.009$ $P = 0.785$ $\Sigma w = 0.180$	$\beta = -0.812$ $P = 0.968$ $\Sigma w = 0.220$
B) Changing density dependence	$\beta = \mathbf{0.366}$ $P = \mathbf{0.002}$ $\Sigma w = \mathbf{0.535}$	$\beta = 0.084$ $P = 0.501$ $\Sigma w = 0.100$	$\beta = \mathbf{0.423}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{0.945}$	$\beta = 0.111$ $P = 0.174$ $\Sigma w = 0.250$	$\beta = -17.53$ $P = 0.664$ $\Sigma w = 0.145$
C) Changing driver sensitivity	$\beta = -0.011$ $P = 0.908$ $\Sigma w = 0.220$	$\beta = 0.078$ $P = 0.432$ $\Sigma w = 0.185$	$\beta = -0.283$ $P = 0.133$ $\Sigma w = 0.155$	$\beta = \mathbf{0.742}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{0.960}$	$\beta = 29.289$ $P = 0.315$ $\Sigma w = 0.260$
D) Unequal dispersal	$\beta = \mathbf{0.064}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{0.970}$	$\beta = -0.002$ $P = 0.764$ $\Sigma w = 0.165$	$\beta = -0.020$ $P = 0.882$ $\Sigma w = 0.105$	$\beta = 0.005$ $P = 0.882$ $\Sigma w = 0.225$	$\beta = \mathbf{1.223}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{1.000}$
Combined mechanisms (see caption, main text)	$\beta = \mathbf{0.407}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{1.00}$	$\beta = \mathbf{0.147}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{0.850}$	$\beta = 0.203$ $P = 0.348$ $\Sigma w = 0.190$	$\beta = -0.055$ $P = 0.297$ $\Sigma w = 0.190$	$\beta = \mathbf{1.068}$ $P < \mathbf{0.001}$ $\Sigma w = \mathbf{0.970}$

The combined scenario involved unequal dispersal and two operating environmental drivers, each affecting the populations equally and having different spatial structures. Model coefficients are denoted β . P -values, based on 1000 permutations, are for tests comparing the 5-predictor model to the model with the predictor in the column header removed. Variable importance (Σw) is quantified by summing, over all models containing each variable, model weights generated using the leave-n-out resampling procedure (see text and Appendix S4 for details).

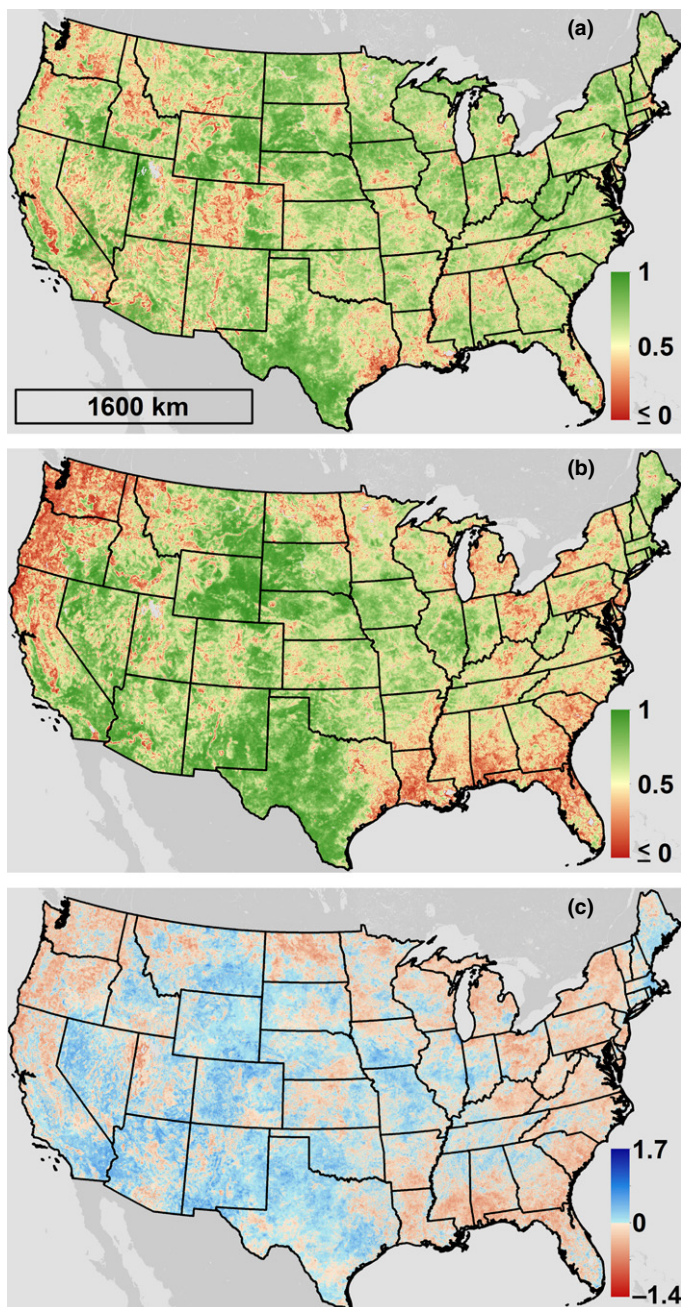


Figure 2 Geography of synchrony of annual maximum normalised difference vegetation index for (a) 1989–1998; (b) 2006–2015; and (c) change in synchrony between era 1 (1989–1988) and era 2 (2006–2015). Positive values in c indicate increases in synchrony from the 1989–1998 period to the 2006–2015 period. See text for details.

underscores that geography of synchrony is a conspicuous feature of these data. There are not only regions of very low synchrony (the Pacific Northwest and California's Central Valley), but also regions of extremely high synchrony (south-west Texas). Major urban areas commonly have low synchrony, but areas dominated by other land cover types are in some locations synchronised and in others asynchronous.

Mapping can be used to infer potential drivers of synchrony. If an environmental factor (e.g. temperature or

precipitation) is driving synchrony in a biological variable through Moran effects, then synchrony maps for the driver should resemble synchrony maps for the biological variable. Similarity of maps can be tested formally using spatial statistics (Defriez & Reuman *in press a,b*). This approach is similar in concept to attempts by earlier studies to attribute causes of synchrony based on similarity in patterns of distance decay between population and environmental synchrony (Koenig 2002; Koenig & Liebhold 2016), an approach that met with limited success (Liebhold *et al.* 2004; Abbott 2007). The new approach is more effective because it uses detailed geographical information for inference. For instance, Defriez & Reuman (*in press a,b*) inferred drivers of synchrony in terrestrial and oceanic primary production. This approach requires data that are highly spatially resolved relative to their geographical extent. Such data sets are increasingly available through remote sensing. There are also manually collected but spatially extensive data sets for plankton (Batten *et al.* 2003; California Cooperative Oceanic Fisheries Investigations 2016), birds (Koenig 2001; Koenig & Liebhold 2016), insect pests (Potter & Paschke 2014) and other taxa.

APPLICATION: MEASURING CHANGES IN SYNCHRONY

Recent work demonstrating changes in synchrony (Allstadt *et al.* 2015; Sheppard *et al.* 2015; Defriez *et al.* 2016; Koenig & Liebhold 2016) suggests that its geography may also change. Changes in geographies of synchrony can be evaluated, for instance, using time-windowed versions of the analysis of the previous section. We mapped synchrony of annual maximum NDVI for 2006–2015 (Fig. 2b) and differenced our time-windowed maps to show changes (Figs 2c).

Synchrony declined on average between 1989–1998 and 2006–2015 (mean difference = -0.029) but changes were highly variable (standard deviation of differences = 0.235). Regional patterns of change are also apparent: synchrony declined markedly in the Pacific Northwest and much of the eastern seaboard, but commonly increased in central USA (Fig. 2c). Much of the Colorado Rockies saw an increase in synchrony. To our knowledge, this is the first analysis to reveal temporal changes in geography of synchrony. Koenig & Liebhold (2016) examined changes in synchrony of weather and bird populations using traditional distance-based analyses. They emphasise the potential conservation importance of the changes they observed. Implications of spatial synchrony for conservation and other human concerns are potentially great. More detailed understanding of how, where and why synchrony changes are needed.

SYNCHRONY NETWORKS AND MODULARITY

We demonstrate a second approach to the geography of synchrony using network graphs. In this approach, network nodes/vertices represent locations at which time series are available, and edges/links represent strength or statistical significance of synchrony between locations (Bollobas 1998; Kolaczyk & Csardi 2014). To our knowledge, synchrony networks are a new type of ecological network. Food web studies

(Pimm *et al.* 1991; Proulx *et al.* 2005; Allesina *et al.* 2008), landscape genetics (Dyer 2015) and other areas of ecology have greatly benefited from network approaches, and we believe the study of synchrony can also benefit.

A primary advantage of a network approach is that it opens the study of spatial synchrony to network mathematics. We identified some metrics and other network characteristics commonly used in the network literature that have meaning for synchrony networks (Table 2). Myriad other approaches to analysing graph structure exist, and it is likely that many can be applied to synchrony networks, and others can be developed. Since our applications of networks to synchrony are initial demonstrations only, for simplicity we treated synchrony networks as unweighted graphs. Weighted networks may also be useful, for instance, in cases with substantial anisotropy.

A potentially common type of geography of synchrony, represented in our simulations (section ‘Application: Inference of the Causes of Synchrony’, Fig. 1), is the presence of groups of locations having high within-group and low between-group synchrony. These groups correspond to ‘communities’ or ‘modules’ in graph theory. Our simulations indicate that modules can arise from several mechanisms, and the modular structure of a network may help infer causes of spatial variation in synchrony. Modules may be geographically compact, or dendritic, or comprised of disconnected components, revealing complex habitat structure or geographically complex effects of synchronising influences. Module detection methods can detect modules of any geographical shape. There are at least three major types of module detection method: (1) techniques descended from the original definition of modularity and the betweenness-based method of Girvan & Newman

(Girvan & Newman 2002; Newman 2006; Fletcher *et al.* 2013); (2) methods based on random walks (Rosvall & Bergstrom 2008); and (3) ‘spectral clustering’ methods reviewed by Von Luxburg (2007). It is yet unclear which will be most suitable for the study of synchrony networks.

APPLICATION: THE ECOLOGY OF THE GYPSY MOTH

To demonstrate a network approach to synchrony, we constructed synchrony networks from data on gypsy moth outbreaks in the northeastern United States from 1975 to 2014. Data consist of annual time series of area defoliated by gypsy moth in sixty-three $64 \times 64 \text{ km}^2$ grid cells covering the region infested by the gypsy moth circa 1975. Defoliation maps were constructed from aerial surveys (Peltonen *et al.* 2002). Synchrony between location pairs was measured using the power-normalised real part of the cross-wavelet transform (Grinsted *et al.* 2004). This quantity is a sensible synchrony metric because it takes larger values when the magnitudes of oscillations are correlated through time and oscillations are in phase. The timescale specificity of wavelet statistics is also an advantage. We explored whether the geography of synchrony is timescale dependent by computing synchrony separately over fluctuation periods of 2–4 years (‘short’ timescales) and 4–12 years (‘long’ timescales). We linked pairs of nodes having statistically significant synchrony, and used colour to indicate the degree of synchrony (Fig. 3). Data processing, wavelet analyses and significance testing are detailed in Appendix S6.

Comparing the short- and long-timescale networks of gypsy moth synchrony (Fig. 3) shows that the strength of synchrony and its geography are both timescale dependent. The long-

Table 2 A selection of established characteristics and quantitative metrics associated with network graphs, and their relevance to the geography of synchrony

	Meaning and reference to formal definition	Relevance to synchrony
Graph characteristic		
Modularity	The presence of groups of vertices (modules) having high within-group connectedness and low between-group connectedness (Newman 2006; Martín González <i>et al.</i> 2012; Fletcher <i>et al.</i> 2013; Krzakala <i>et al.</i> 2013; Peterman <i>et al.</i> 2016)	Modules indicate synchronous collections of locations. Some algorithms (Newman 2006; Krzakala <i>et al.</i> 2013) also indicate the strength of membership of each node in its module
Global (graph-wide) metrics		
Degree distribution	The frequency distribution of vertex degree (Kelly <i>et al.</i> 2012; Kolaczyk & Csardi 2014). Vertex degree is the number of edges incident on each vertex (Brandes & Erlebach 2005; Kolaczyk & Csardi 2014)	Different degree distributions imply different geographies of synchrony. For example, a Poisson distribution suggests that synchrony lacks spatial structure (Brandes & Erlebach 2005; Kolaczyk & Csardi 2014); a power-law suggests synchrony propagates from a few ‘hubs’ (Brandes & Erlebach 2005; Kolaczyk & Csardi 2014)
Global transitivity	The probability that adjacent vertices of a vertex are themselves connected, considering all vertices (Wasserman & Faust 1994; Opsahl & Panzarosa 2009)	Transitivity indicates the tendency to cluster into synchronous groups (Kolaczyk & Csardi 2014)
Local (single-vertex) metric		
Centrality	Centrality metrics quantify the importance of vertices to the network (Brandes & Erlebach 2005). Vertex degree is one such metric; another, betweenness, quantifies the frequency with which a vertex lies along shortest paths between other vertices (Newman 2010)	High centrality implies a ‘hub’ of synchrony

For simplicity, definitions in the table apply to unweighted graphs, but metrics are easily extended to weighted graphs.

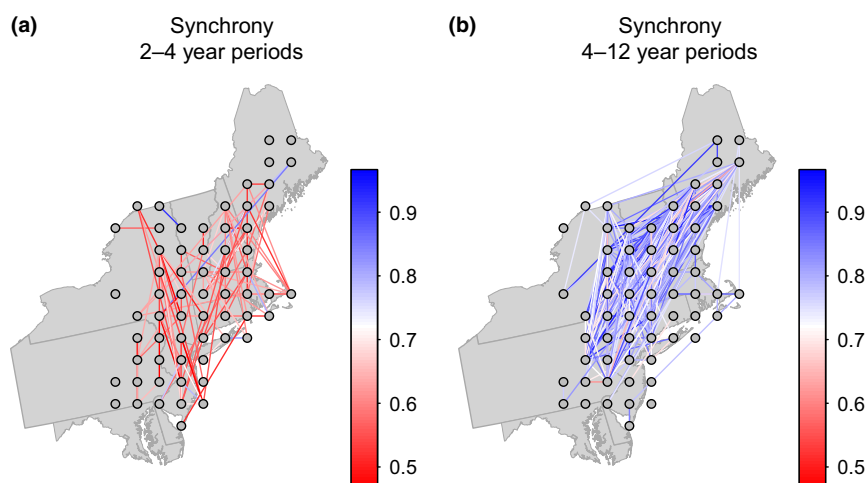


Figure 3 Timescale-specific synchrony networks for gypsy moth defoliation. Only statistically significant ($\alpha = 0.01$, see Appendix S6 for methods) edges are shown. Colour indicates values of the power-normalised real part of the cross-wavelet transform, averaged over respective timescales, but only the topological (unweighted) network structure (ignoring colour) was used in subsequent analyses, for simplicity. Colours were for visual comparisons only.

timescale network (Fig. 3b) is more densely connected, with links concentrated among inland locations. The short-timescale graph (Fig. 3a) has fewer and more uniformly distributed links. At long timescales, 314 location pairs were significantly synchronous ($\alpha = 0.01$), but only 104 pairs were significantly synchronous at short timescales, and less than 30% of these were also significantly synchronous at long timescales. Because of the greater synchrony at long timescales and because the dominant oscillation periods for gypsy moths are known to range between about 4 and 10 years (Johnson *et al.* 2006; Haynes *et al.* 2009b), we focus on the long timescale network.

We applied three graph theoretic techniques to the long-timescale synchrony network: vertex degree distribution, transitivity and a measure of centrality. Vertex degree measures the number of edges incident on each vertex. Comparing the statistical distribution of vertex degree across vertices with distributions arising from random or null-model graphs yields insight into graph structure (Kelly *et al.* 2012; Kolaczyk & Csardi 2014). Transitivity, also called the clustering coefficient, is the probability that the vertices adjacent (connected) to each vertex are themselves connected, and can be applied to single nodes or the graph as a whole. We consider the whole-graph metric. Centrality is a class of metrics quantifying the importance of a vertex or link to the network (Brandes & Erlebach 2005). We used vertex degree itself as a centrality metric because a location that is synchronous with many other locations (high vertex degree) is of intrinsic interest and can be considered ‘central’ in our context.

To develop statistical tests for geography of synchrony for network graph characteristics, we compared the long-timescale empirical synchrony network to a distribution of random graphs generated under a null hypothesis of isotropic distance decay of synchrony. We use this null hypothesis because of our interest in deviations from this well-studied pattern (Bjørnstad & Falck 2001). We simulated 1000 realisations of a process that preserved the number and location of vertices and generated edges randomly with distance-dependent

probabilities. The dependence of edge probability on distance was conditioned empirically through logistic regression (Appendix S7). Other null hypotheses may be appropriate for other research goals, e.g. Erdos–Renyi random graphs for which m edges are distributed among n vertices entirely randomly (Erdos & Renyi 1959), thus providing a null hypothesis of no spatial structure at all, even excluding distance decay.

The degree distribution for the long-timescale gypsy moth synchrony network had notable differences from degree distributions of networks generated from the null model. The empirical network had larger numbers of sparsely and highly connected nodes than the null model (Fig. 4a). Transitivity (τ) was greater for the empirical synchrony network ($\tau = 0.731$) than for all 1000 randomised graphs, indicating that the network contains components that are more densely connected than expected based on distance alone. These summary results show that gypsy moth synchrony has a meaningful geography. To display details of the geography, we identified nodes with vertex degrees significantly higher than the distributions of their degrees under the null model. These ‘hubs’ are especially important locations for synchrony (Fig. 4b).

One hypothesis consistent with the above findings is that the long-timescale gypsy moth synchrony network consists of network ‘modules’ (sets of locations) having relatively strong within-set synchrony but weak between-set synchrony. We examined evidence for such structure using wavelet clustering (Rouyer *et al.* 2008), a technique that uses information at all timescales. Strength of cluster membership for each location was calculated as in Fletcher *et al.* (2013). The gypsy moth synchrony network contained two distinct clusters, with Cluster 1 largely near the coast and Cluster 2 largely inland (Fig. 5a).

Post-hoc analyses generally should be performed to interpret the ecological meaning of clusters and to determine whether mathematical differences between them are ecologically important. We used for this purpose mean time series and wavelet mean fields (Sheppard *et al.* 2015). The wavelet mean field is an average of normalised wavelet transforms. If at a given

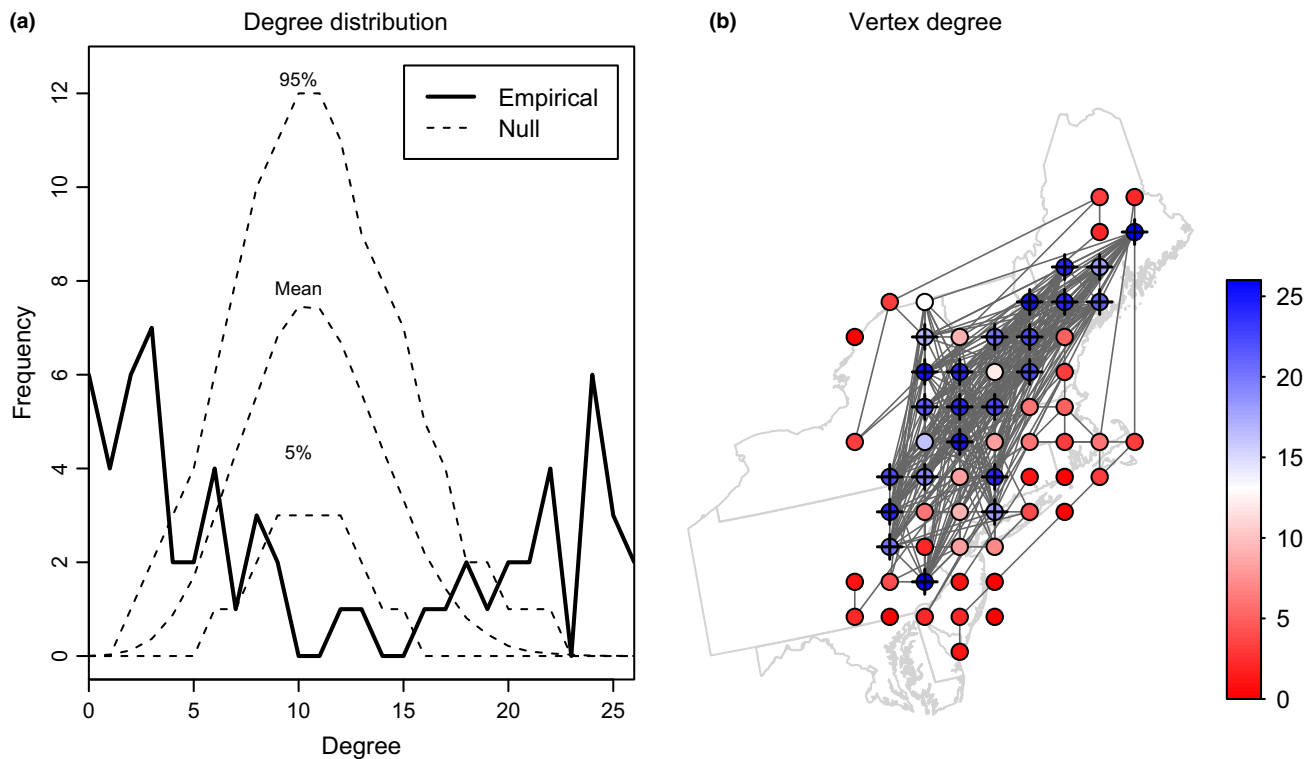


Figure 4 (a) The empirical degree distribution (solid line) of the long-timescale gypsy moth synchrony network (shown in Fig. 3b), compared to the degree distributions of 1000 randomised networks under a null hypothesis of isotropic distance decay in synchrony (edge probability). (b) The degree of each vertex (colour). Nodes with a '+' have significantly high degree ($\alpha = 0.05$) using the same null hypothesis. See main text and Appendix S7 for details.

time and timescale, oscillations have similar phase, and are thus synchronised, the magnitude of the wavelet mean field is large, whereas if the phases are unrelated the magnitude is small. Thus, the wavelet mean field for a cluster provides a time- and timescale-specific depiction of synchrony.

Differences between clusters were evident in (5th root transformed to improve normality; Allstadt *et al.* 2013) mean time series (Fig. 5c,e) and wavelet mean fields (Fig. 5d,f) for each cluster. As has previously been observed, outbreaks occurred on 4–5 and 8–10 year cycles (Bjørnstad *et al.* 2010; Haynes *et al.* 2012; Allstadt *et al.* 2013). Clusters differ in the relative strength of 4–5 year vs. 8–10 year oscillations, and in the severity of outbreak decline in the second half of the study period. Cluster-average time series (Fig. 5c,e) depict the synchronous component of oscillations in each of the two clusters, since non-synchronous, local oscillations tend to cancel out in average time series. Cluster 1 exhibits synchronous 4–5 year oscillations and the strongest recent outbreaks, which shifted to longer timescales beginning in the 1990s. Cluster 2 shows stronger synchrony at 8–10 year timescales and a decline in recent outbreak amplitude.

We next used matrix regression with our new model selection procedures (section 'Application: Inference of the Causes of Synchrony', Appendix S4) to assess how two mechanisms underlying geography of synchrony, spatial structure in the synchrony of environmental drivers (mechanism A) and differences in density dependence (mechanism B) affect gypsy moth defoliation synchrony. Our analyses build on an earlier analysis of geographical variation in

gypsy moth synchrony (Haynes *et al.* 2013). As in Haynes *et al.* (2013), we use matrices of weather synchrony, forest composition similarity and spatial proximity to predict patterns in a matrix of gypsy moth synchrony. We also use similarity in density dependence, calculated from estimated AR(2) coefficients (as in section 'Application: Inference of the Causes of Synchrony' for the simulations, and described in Appendix S3). Weather was represented by the first two principal components (PC1 and PC2) resulting from 36 weather variables (monthly average minimum temperature, monthly average maximum temperature, and monthly total precipitation) at each location from 1975 to 2014. As for the gypsy moth, synchrony was measured as the normalised real part of the cross-wavelet transform, averaged over 4–12 year timescales. Because a recent report raised concerns that interpolated climate products (including PRISM data used by Haynes *et al.* 2013) may be inaccurate for precipitation (Behnke *et al.* 2016), we used weather station data obtained from the US Historical Climate Network (Easterling *et al.* 1996). Similarity in forest type was determined by computing the proportion of each grid cell comprised of 7 forest types using maps produced by Ruefenacht *et al.* (2008) and taking the Mahalanobis distance between grid cell pairs (Haynes *et al.* 2013). Distances were converted to similarities using $1 - (x/\max(x))$. Appendix S8 provides details of the data preparation and model selection procedures.

The best predictor of gypsy moth synchrony was synchrony in PC2 (Table 3), which primarily reflected variation in precipitation (Haynes *et al.* 2013). Similarity in forest type may also play a secondary role in generation of spatial patterns of

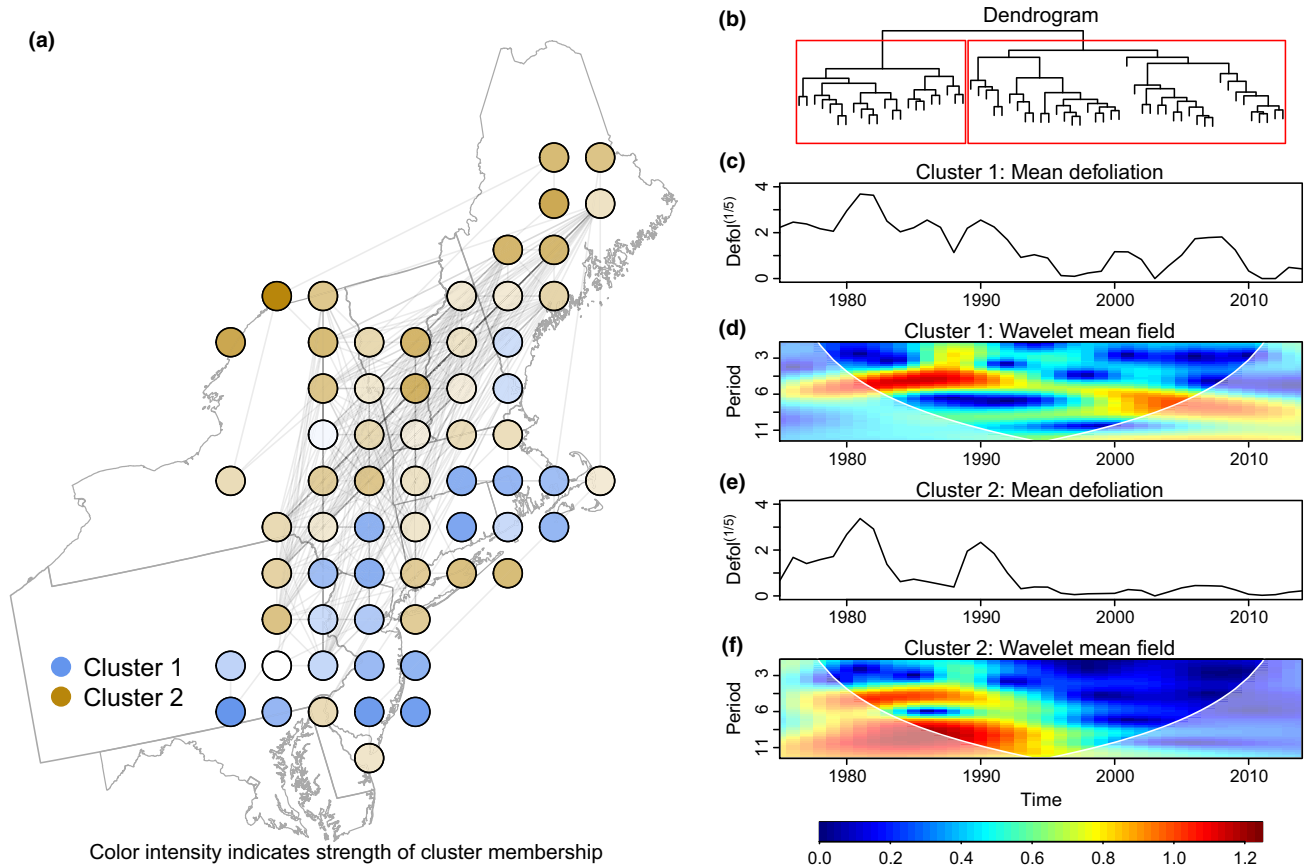


Figure 5 Module structure in the gypsy moth network. Panel (a) cluster identity (colour) and membership strength (shading); (b) wavelet clustering dendrogram; (c, e) mean defoliation time series for each cluster; (d, f) wavelet mean field magnitudes for each cluster.

synchrony: the top model by cross-validation weights contained synchrony in PC2 and forest type similarity. Previously, forest type has been linked to geographical patterns in density dependence (Liebhold *et al.* 2006) and outbreak periodicity (Haynes *et al.* 2009b); these effects are hypothesised to result from influences of natural enemies (Haynes *et al.* 2009a, 2013). Although statistically significant, the top model had only $R^2 = 0.153$, suggesting that unidentified factors play large roles in the geography of gypsy moth synchrony. We examined module structure in the PC2 synchrony network, but this did not obviously correspond to patterns of gypsy moth synchrony (Appendix S9).

Table 3 Matrix regression coefficients (β), P -values and variable importance weights (Σ_w) of predictors of gypsy moth synchrony at long (4–12 years) timescales. Bold font indicates statistically significant effects.

Predictor	β	P	Σ_w
Density dependence similarity	0.156	0.260	0.410
Forest type similarity	−0.222	0.198	0.545
Synchrony in PC1 scores	−0.114	0.787	0.245
Synchrony in PC2 scores	0.699	0.003	0.775
Proximity	0.181	0.260	0.455

Coefficients and P -values come from the full model including all predictors. Importance weights were generated using model selection methods (Appendices S4 and S8).

DISCUSSION

Despite long-standing interest in synchrony, few studies have recognised the geography of synchrony and investigated its causes and consequences, and few studies have leveraged the geography of synchrony to understand ecological processes. We have here synthesised several pioneering papers and extended prior work by: (1) showing conceptually and theoretically how four mechanisms can generate geographies of synchrony; (2) documenting complex and pronounced geographies of synchrony in important study systems, and showing that these patterns can exhibit ‘hubs’ and ‘modules’, can be timescale specific, and can change through time; and (3) demonstrating several methods capable of revealing the geography of synchrony and using it to understand the causes and nature of synchrony, and organism ecology. The potential for geographies of synchrony to improve the attribution of drivers of synchrony is a promising avenue of research; identification of drivers of synchrony has been a long-standing challenge in population ecology (Ranta *et al.* 1995; Liebhold *et al.* 2004). Further, we introduced a new type of network, the synchrony network, which we believe may be very useful in future studies of spatiotemporal dynamics.

We examined mechanisms of the geography of synchrony that seem likely to be widespread and for which there is empirical support, but there may be other mechanisms. Our

gypsy moth analyses provided evidence that spatial patterns in the synchrony of environmental drivers (mechanism A) can underlie geographies of synchrony (Table 3). Previous studies of the gypsy moth indicate that differences in density dependence (mechanism B) may be important as well (Liebhold *et al.* 2006). Defriez & Reuman (*in press a*) found between-continent heterogeneity in Moran effects resulting from temperature and precipitation, supporting our hypothesis that geography of synchrony can arise because dynamics in different locations are affected by different drivers (mechanism C). Bellamy *et al.* (2003) and T L Anderson *et al.* (unpublished data) found effects of landscape structure on synchrony of bird and plankton populations, respectively, consistent with unequal rates of dispersal between populations (mechanism D). One additional possible mechanism, yet to be empirically demonstrated, is that population fluctuations may be synchronised by multiple drivers of synchrony, which may interact, and the nature of the interactions themselves might change spatially.

Our work focused on settings for which dynamics are adequately approximated by linear models. Although Moran effects and dispersal can produce synchrony in non-linear models (Abbott 2007; Haynes *et al.* 2009a; Vasseur & Fox 2009), strongly non-linear dynamics may complicate detection and attribution of mechanisms of synchrony and its geography through the emergence of self-organised spatiotemporal patterns (Hassell *et al.* 1991; Sole *et al.* 1992; Bjørnstad 2000; Bjørnstad & Bascompte 2001). Although linear approaches have a long and successful history in ecology and represent a firm starting place (Royama 1992), future theoretical study should address the robustness of our approaches to deviations from linear population dynamics.

For the gypsy moth, we showed that synchrony and its geography can be timescale specific, and we demonstrated the existence of both 'hubs' and 'modules' of synchrony. Future analysis will reveal the extent to which such features are common of a wide range of organisms. Prior to our study, timescale specificity of spatial synchrony had been demonstrated in epidemiological systems (Grenfell *et al.* 2001; Viboud *et al.* 2006), lab systems (Vasseur & Fox 2009), insects (Bjørnstad *et al.* 2008; Sheppard *et al.* 2015) and marine plankton (Defriez *et al.* 2016), although these studies did not explore geographies of synchrony in the explicit way advocated here. We showed that frequency specificity and geography of synchrony can be interacting features. Hubs of synchrony could, in principle, correspond to areas of high population density, or reveal areas acting as major sources of migrants. Synchrony hubs may thus have importance for invasion ecology. Hubs may reveal epicentres or start points of outbreaks (Grenfell *et al.* 2001) and thus may be important for pest and disease control. Network module boundaries may correspond with substantial spatial changes in dynamics, and the location of these boundaries may yield important insights into processes regulating populations. For instance, for gypsy moth, modules may relate to transitions from oak-hickory and oak-pine forest types to maple-beech-birch types (Johnson *et al.* 2006; Liebhold *et al.* 2006; Haynes *et al.* 2013). Hubs and modules can be revealed only with a detailed spatial approach.

Secular changes have recently been observed in aspects of synchrony, including in its distance decay, timescale structure and overall strength (Post & Forchhammer 2004; Allstadt *et al.* 2015; Sheppard *et al.* 2015; Defriez *et al.* 2016; Koenig & Liebhold 2016; Shestakova *et al.* 2016). Adding to these results, we showed large temporal changes in the geography of synchrony for terrestrial primary production in the United States. Our findings may have implications for regional food and forest production, carbon cycling, global change biology and other applications. It is the synchronous components of local fluctuations that disproportionately affect regional averages of any quantity: non-synchronous components tend to cancel in the regional total, but synchronous fluctuations combine to have large effects. Therefore, changes in synchrony can lead to changes in time series of regional productivity, even when statistical properties of local time series considered in isolation remain unchanged. In the case of a crop, such changes may lead to changes in the variability in regional production. Regional carbon uptake from the atmosphere is also related to the total net production of locations in the region, which is affected by synchrony of local primary production time series. These implications of changes in synchrony and its geography focus on the terrestrial productivity example, but changes in synchrony are also important for conservation (Koenig & Liebhold 2016) and pest management (Bjørnstad *et al.* 2008; Sheppard *et al.* 2015). Changes in the geography of synchrony may affect spatial aspects of these applications. Some observed changes in synchrony seem likely related to (Post & Forchhammer 2004; Koenig & Liebhold 2016) or have already been convincingly attributed to climatic change (Sheppard *et al.* 2015; Shestakova *et al.* 2016). Whether geographical changes in synchrony are linked to global change is unknown but important.

Several factors influence whether mapping synchrony (Fig. 2) or synchrony networks (Figs 3–5) is the better approach in application to other systems. Both correlations and spectral tools can be used with either approach. The two approaches investigate slightly different questions: synchrony maps ask how the amount of local or regional synchrony varies geographically, while synchrony networks focus on which location pairs are synchronised. Synchrony maps seem most applicable when observation locations are numerous and spatially uniform. The rise of remote sensing makes such data increasingly available. Neighbourhood averaging obscures information about pairwise relationships, but this could be a strength rather than a weakness for large datasets. Synchrony network approaches, probably better suited to data sets with fewer locations, retain a complete set of information about synchrony. Numerous well-developed tools from network mathematics (Bollobas 1998; Brandes & Erlebach 2005) strengthen characterisations of synchrony network structure. Mapping synchrony and synchrony networks both have potential to yield new insights into spatial synchrony.

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AUTHORSHIP

JAW and DCR conceived of the study, designed and implemented models and analyses, and drafted the manuscript; LWS and TLA developed methods and contributed to study design; JHK performed the vegetation synchrony analyses; ONB contributed to methods development; and AML contributed data and input on study design. All authors contributed substantially to development of ideas, interpretation of results and revision of the manuscript.

STATEMENT ON DATA AVAILABILITY

AVHRR data are available online at <http://www.class.ncdc.noaa.gov/>. Gypsy moth defoliation data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p8cv8>

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