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Micro-scale geography of synchrony in a serpentine plant community

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Abstract

1. Fluctuations in population abundances are often correlated through time across multiple locations, a phenomenon known as spatial synchrony. Spatial synchrony can exhibit complex spatial structures, termed 'geographies of synchrony', that can reveal mechanisms underlying population fluctuations. However, most studies have focused on spatial extents of 10s to 100s of kilometres, making it unclear how synchrony concepts and approaches should apply to dynamics at finer spatial scales.
2. We used network analyses, multiple regression on similarity matrices, and wavelet coherence analyses to examine micro-scale synchrony and geographies of synchrony, over distances up to 30 m, in a serpentine grassland plant community.
3. We found that species' populations exhibited a geography of synchrony even over such short distances. Often, well-synchronized populations were geographically separate, a spatial structure that was shaped mainly by gopher disturbance and dispersal limitation, and to a lesser extent by relationships with other plant species. Precipitation was a significant driver of site- and community-wide temporal dynamics. Gopher disturbance appeared to drive synchrony on 2- to 6-year timescales, and we detected coherent fluctuations among pairs of focal plant taxa.
4. *Synthesis*. Micro-geographies of synchrony are an intriguing phenomenon that may also help us better understand community dynamics. Additionally, the related geographies of synchrony and coherent temporal dynamics among some species pairs indicate that incorporating interspecific interactions can improve understanding of population spatial synchrony.

KEYWORDS
community stability, compensatory dynamics, disturbance, gopher, grassland, plant population and community dynamics, spatial synchrony

1 | INTRODUCTION

Spatially disjunct populations of a given species often fluctuate in tandem, a phenomenon known as spatial synchrony (Liebhold, Koenig, & Bjørnstad, 2004). Spatial synchrony is a fundamental aspect of population dynamics that can result from any of three processes (Liebhold et al., 2004): spatially correlated exogenous environmental drivers, that is, Moran effects (Moran, 1953); dispersal; or interactions with a spatially synchronous species, such as a predator or parasitoid. Recent work has highlighted that spatial synchrony can exhibit geographic structure, in which the degree of synchrony between locations varies not only as a decreasing function of the distance between the locations (a common pattern recognized for decades), but also in other ways that are more complex and more informative (Walter et al., 2017). Such geographies of synchrony can reflect multiple causes related to mechanisms of synchrony itself (spatial patterns in environmental drivers or dispersal) and to factors that modify the strength of synchrony between locations, but do not cause it (as diagrammed in Supporting Information S1). These include spatial differences in population density dependence, and differences in population sensitivities to environmental drivers (Walter et al., 2017). Complex geography is increasingly recognized as a common and important aspect of synchrony (Anderson et al., 2017; Defriez & Reuman, 2017a, 2017b; Gouveia, Bjørnstad, & Tkadlec, 2016; Haynes, Bjørnstad, Allstadt, & Liebhold, 2013; Haynes, Walter, & Liebhold, 2019; Walter et al., 2017).

Geography of synchrony may, a priori, manifest at small as well as large spatial extents, but until now it has been studied almost entirely across spatial extents from 10s to several 100s of km; the lower spatial limits of the geography of synchrony have not been explored. The spatial extent of study is likely important for ascertaining drivers of synchrony itself and mechanisms of geographic variation in synchrony, which may or may not be the same. Since climate and weather, major sources of Moran effects, are near-identical over small spatial extents, micro-geographies of synchrony should reflect mechanisms such as habitat heterogeneity, local disturbance and dispersal limitation. At all spatial scales, reductions in synchrony arising from such processes may enhance metapopulation stability and persistence by reducing variance in aggregate abundance (or related quantities) across sites (Heino, Kaitala, Ranta, & Lindström, 1997; Schindler, Armstrong, & Reed, 2015; Walter et al., 2017). Micro-geographies of synchrony, if they occur, might be particularly important for the persistence of species inhabiting rare or isolated habitats (Eklöf, Kaneryd, & Münger, 2012).

The importance of spatial heterogeneity and scaling has also recently been embraced in community ecological research focusing on a different kind of synchrony. In contrast to population ecology, community ecology has typically focused on interspecific synchrony within a locale and its implications for the stability of community-aggregate properties in that locale. For example, a core concept is ‘compensatory dynamics,’ in which asynchrony among species buffers aggregate properties of the community, like total biomass, against population variability (Brown, Downing, & Leibold, 2016; Gonzalez & Loreau, 2009). Recently developed approaches have scaled these concepts spatially by considering interspecific synchrony at the local/plot level and between-plot synchrony at the landscape level (Loreau & de Mazancourt, 2008; Wang, Lamy, Hallett, & Loreau, 2019; Wang & Loreau, 2014, 2016). These approaches have highlighted that asynchrony among plots can increase overall ecosystem stability (Wilcox et al., 2017).

Studying spatial and interspecific synchrony in tandem has the potential to improve understanding of spatiotemporal dynamics of populations and communities. For example, interspecific interactions shaping area-wide spatial synchrony might be revealed by comparing the geographies of synchrony for putatively interacting species. Determining the drivers of spatial synchrony and its geography for multiple members of a community might uncover forces underlying variability in community-wide dynamics.

Here we develop an integrated analytic framework to explore the micro-geography of synchrony, testing the importance of Moran effects, proximity, habitat heterogeneity, local disturbance and interspecific interactions for shaping population spatial synchrony on very small spatial scales (Figure 1). We combine spatially explicit approaches (Haynes et al., 2013; Walter et al., 2017) with spectral approaches (Sheppard, Bell, Harrington, & Reuman, 2016; Sheppard, Defriez, Reid, & Reuman, 2019) to address our questions at short and long timescales. We use 33-year time series from a serpentine grassland community at the Jasper Ridge Biological Preserve (San Mateo, CA). Dominant species at the site have exhibited highly variable and spatially synchronous abundance patterns, presumably in response to a highly variable climate (Hobbs & Mooney, 1995; Hobbs, Yates, & Mooney, 2007). We specifically address the following questions for the system: (Q1) Do geographies of synchrony occur on small spatial scales, so-called ‘micro-geographies’ of synchrony? (Q2) What causes micro-geography of synchrony in this system, and are the causes of micro-geography of synchrony also drivers of synchrony itself, or instead factors that modify the strength of synchrony generated by other drivers? (Q3) What are the potential implications of micro-geographies of synchrony for ecological stability? To our knowledge, this study is the first to investigate potential ‘micro-geographies’ of synchrony and their causes and consequences; the spatial extent here is about 30 m, much smaller than prior studies of the geography of synchrony. Our study is also a novel way of investigating the important new topic of interrelationships between community synchrony/compensatory dynamics, spatial synchrony and ecosystem stability.

2 | MATERIALS AND METHODS

2.1 | Study site

Data were collected from 1983 to 2015 at the Jasper Ridge Biological Preserve in San Mateo County, California, USA (122°12′W,

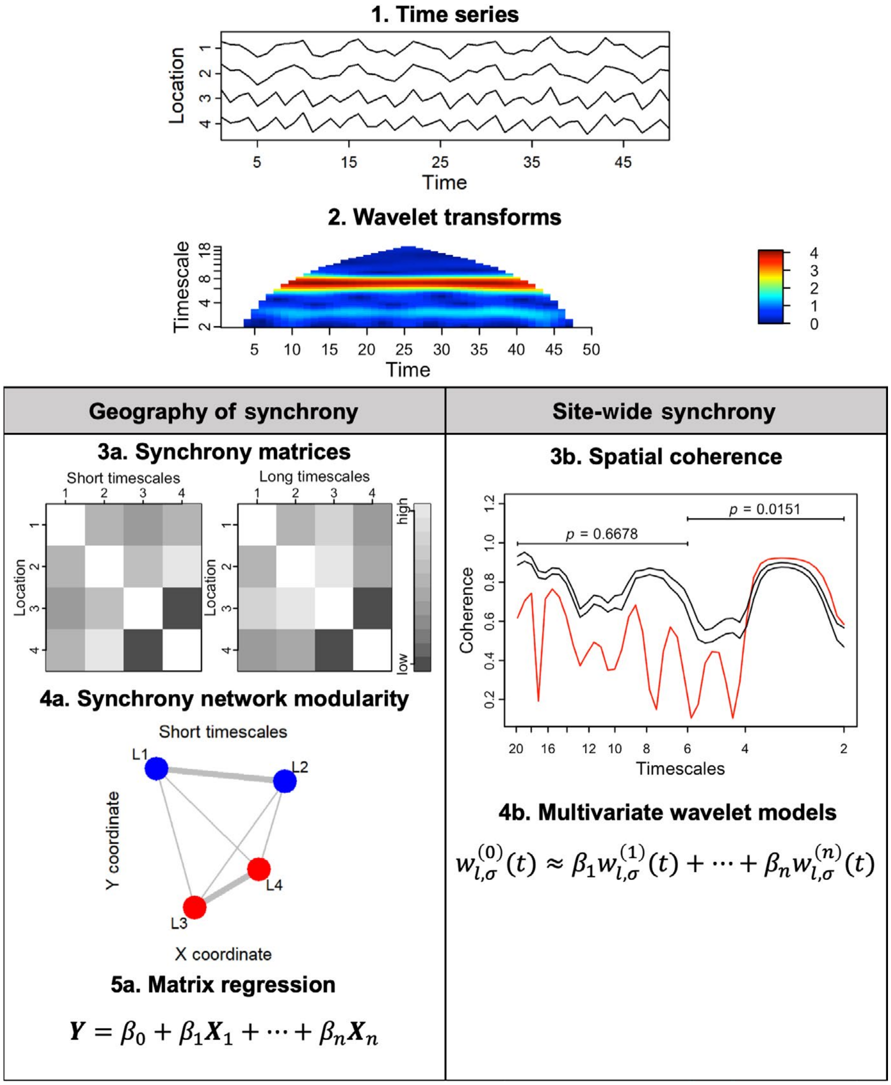

FIGURE 1 Workflow illustration. We begin with time series that for this illustration are a linear combination of periodic signals at 3- and 7-year timescales and white noise (1). The wavelet transform (2) is the basis of parallel analyses focused on geographies of synchrony (a) and on site-wide synchrony (b). Shown here is the wavelet power for location 1, indicating strong periodicity at 7-year timescales and lesser periodic content at 3-year timescales, as constructed. For geographies of synchrony, we use wavelets to generate synchrony matrices for short and long timescales, defined here as 2 to 6 and >6 years, respectively (3a). Synchrony matrices form the basis of synchrony networks, and we use modularity to characterize the tendency for the network to consist of sub-groups having high within-group but low between-group synchrony (4a). We use MRM (5a) to examine potential mechanisms of geography of synchrony. We examine temporal patterns using wavelet spatial coherence (3b), testing statistical significance by comparison with surrogate data representing a null hypothesis of no coherence that preserves auto- and cross-correlation properties of the time series. Multivariate wavelet models (4b) allow us to test simultaneously for the influence of multiple variables. The methods illustrated in 3a and 4a are used to answer Q1; 3b, 4b, and 5a are used to answer Q2

36°25′N). The study site is a serpentine outcrop that bisects the ridge. Typical of serpentine grasslands, the soil is shallow (<40 cm deep), with low nutrient concentrations, high nickel and manganese concentrations and a low calcium:magnesium ratio. The site experiences a Mediterranean climate with mild, wet winters and hot, dry summers. Mean growing season rainfall (September–April) over the study period was 604 mm but varied greatly, from 228 to 1,155 mm. The site is dominated by annual plants (primarily annual forbs and a few annual grasses) that germinate in autumn and set seed in spring and summer.

2.2 | Experimental design

In November 1982, RJH established three permanent experimental treatments at our study site: gopher exclosures, rabbit exclosures and a control. Gopher exclosures were achieved by burying 1 cm mesh to the bedrock, with 30–40 cm of mesh extending above-ground. Rabbit exclosures were created using 2-cm mesh to create a 1 m high fence around the treatment replicate. The experiment was replicated three times in a random-block design. Each treatment replicate was 4 m × 4 m and replicates were separated by 5 m. See Hobbs and Mooney (1991) for full experimental details. The gopher treatment was re-fenced twice in the first 20 years of study; however, the fencing was only partially successful and all replicates were disturbed at some point. As such, the gopher exclosure treatment reduced the frequency of disturbance but did not eliminate disturbance (Hobbs et al., 2007). At the same time, Hobbs et al. (2007) found that the rabbit exclosure treatment experienced elevated amounts of gopher activity. Consequently, we considered the treatments to be effective in that they created communities that experienced a broad range of disturbance frequencies, but we did not assess treatment effects categorically. Instead, we directly measured the level of gopher disturbance a plot experienced each year.

We characterized gopher disturbance, plant species abundance and soil depth in four 1 m × 1 m plots per treatment replicate for a total of 36 plots (3 treatments × 3 replicates per treatment × 4 plots per replicate; see Figure S2 for a plot map). Presence of new gopher mounds was mapped each April from 1983 to 2015. Gopher activity was scored as presence/absence within each 0.25 m × 0.25 m quadrat of the plot; thus, when summed at the plot level, gopher activity ranged on a scale of 0 (no disturbance) to 16 (all areas were disturbed). Species abundance was measured visually as percent cover in early April of each year using cover classes of 1, 2, 5, 10 and increments of 10 thereafter; total cover could be greater than 100 due to canopy structure or <100 due to bare ground. We observed 34 total species at the site, and while their abundances fluctuated over time (Figure 2), their presence was quite stable over the course of the study (Hallett, Farrer, Suding, Mooney, & Hobbs, 2018; Hobbs et al., 2007; Table S1). For these analyses we focused on the six species with the highest average abundances over time: four native annual forbs (*Calycadenia multiglandulosa*, *Lasthenia californica*, *Microseris douglasii*, *Plantago erecta*), a native annual grass *Vulpia microstachys* and a non-native annual grass *Bromus hordeaceus* (nomenclature following Baldwin et al., 2012). In 1983, soil depth was scored within each 0.25 m × 0.25 m quadrat of the plot by pushing a graduated metal probe into the soil until it hit bedrock. This resulted in 16 measures of soil depth per 1 m × 1 m plot, which we averaged.

We used daily precipitation records from Jasper Ridge to characterize rainfall during the study period. Particularly, early in the study, some data were missing in the Jasper Ridge record. When missing values occurred we substituted precipitation data from the Woodside Fire Station (National Center for Environmental Information, ID GHCND: USC00049792), located 3 km to the northwest at 116-m elevation. To characterize growing season rainfall, we summed rainfall from the start of September through the start of April. Rainfall seasonality can affect species dynamics, with fall rainfall affecting germination and winter affecting survival and growth (Dudney et al., 2017; Gulmon, 1992; Hallett, Shoemaker, White, & Suding, 2019; Pitt & Headey, 1978). To capture these dynamics, we characterized fall rain summed from Sept to Nov and winter summed from Dec to Feb. Rainfall was not correlated between seasons (Pearson's correlation coefficient = 0.1). To better characterize patterns of long-term drought, we used the palmer drought severity index (PDSI) for coastal Northern California (Dai & National Center for Atmospheric Research Staff, 2017, State Code 4 in Division 4), averaged over the 7 months of the growing season. PDSI is an index of long-term (≥12 months) drought generally taking values between −10 (dry) and 10 (wet) that incorporates air temperature and a physical water balance model (Dai & National Center for Atmospheric Research Staff, 2017).

2.3 | Analyses: Micro-geography of synchrony

We characterized micro-geographies of synchrony (Q1) using traditional distance-decay (Bjørnstad & Falck, 2001) and newer synchrony

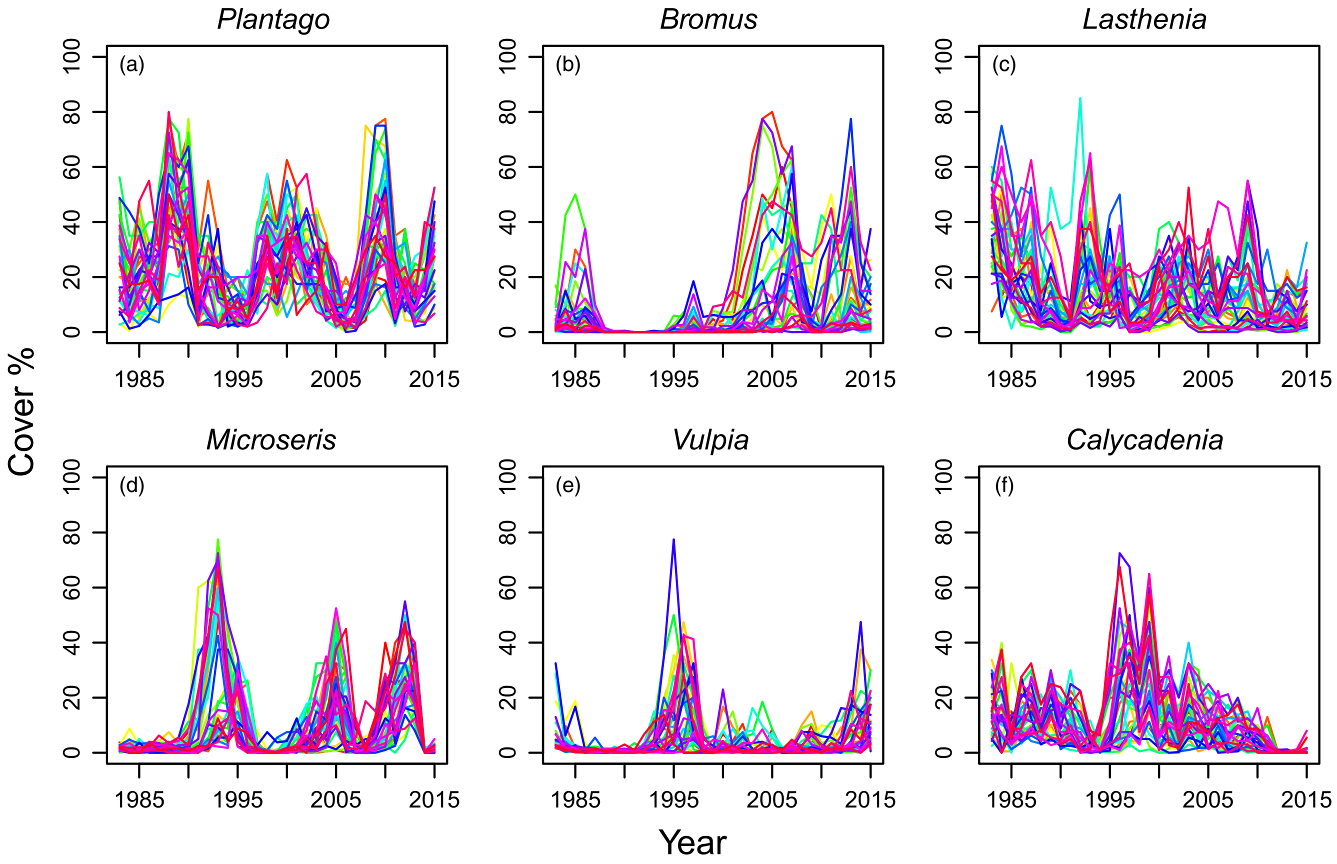

FIGURE 2 Raw data time series for the six focal serpentine plant species at Jasper Ridge Biological Preserve, 1983–2015. Each coloured line represents a plot

network approaches (Walter et al., 2017; Figure 1). Both approaches begin by computing a synchrony matrix, a generalization of the correlation matrix, that is, a square matrix indexed by location, with entries giving the pairwise synchrony between locations. For each plant species and gopher disturbance separately, we quantified synchrony between two locations using a power-normalized integration of the real part of the cross-wavelet transform, which we abbreviate ReXWT. ReXWT can be interpreted as a timescale-specific correlation coefficient. Like standard correlation, ReXWT equals 1 when the magnitudes of oscillations in two time series are perfectly correlated through time and in-phase; ReXWT equals −1 when oscillations are perfectly anti-correlated through time, that is, in anti-phase (peaks in one time series align with troughs in the other). ReXWT is timescale-specific, which can uncover differences in relationships at short timescales (fast oscillations) versus long timescales (slow oscillations). Mathematical details are given in Walter et al. (2017).

Geographies of synchrony were examined at 'short' (2–6 year) and 'long' (>6 year) timescales. Six years was chosen as the dividing line between short and long timescales because preliminary analyses showed that gopher disturbance was particularly synchronous over 2- to 6-year timescales. Taking into account the known importance of gopher disturbance in this system (Hobbs & Mooney, 1985, 1995), our short and long timescale bands also separate timescales in which plant synchrony may be dominated by gopher disturbance from timescales in which other processes (e.g. climate variability, biotic interactions) may dominate. For each pair of plots, the timescale-specific ReXWT was integrated across the short and long timescale bands to produce estimates of short- and long-timescale synchrony for the pair.

Over each timescale band, we characterized the distance decay of synchrony by fitting a smoothing spline to pairwise synchrony versus inter-plot distance, and performing a standard bootstrap resampling procedure to estimate confidence intervals (Bjørnstad & Falck, 2001). We also examined the structure of synchrony networks, which depict synchrony between locations as a network graph in which nodes correspond to locations and edges (links) denote synchrony between locations. To characterize synchrony network structures, we evaluated their modularity, that is, the presence of groups of locations having relatively high within-group synchrony but low between-group synchrony, for each plant species and for gopher disturbance. We used undirected networks with weights given by the ReXWT between each pair of plots. To detect modules, we used an extension of the eigenvalue-based method of Newman (2006) that accommodates networks with positive and negative weights (Supporting Information S3). One advantage of this method is that it has a built-in criterion for stopping subdivision of the network into additional modules, whereas many other clustering algorithms require a priori choice of the number of groups, even though the true number is rarely known.

We tested whether modules were statistically significant by comparing the modularity statistic for each empirical plant synchrony network to a distribution of values generated using 10,000 parametric bootstrap simulations representing a null hypothesis of no modular structure. Network modularity was considered statistically significant if the empirical value was >95% of the modularity values for these surrogate datasets. Details of the parametric bootstrapping procedure are provided in Supporting Information S4.

Prior to analysis, each time series was linearly detrended and scaled to have mean = 0 and variance = 1. An optimal Box-Cox transformation was applied to normalize distributions of plant time series. These pre-processing steps were necessary to meet assumptions of significance testing procedures used to address parts of Q2 and were applied across all analyses for consistency. Gopher disturbance time series could not be pre-normalized, which necessitated adjustments to significance testing procedures for wavelet methods (see below). Data cleaning, wavelet analyses and module detection was carried out using the WSYN package (Reuman, Anderson, Walter, Zhao, & Sheppard, 2019) for the R programming language (R Core Team, 2018).

2.4 | Analyses: Causes of micro-geography of synchrony

We used multiple regression on similarity matrices (MRM; Haynes et al., 2013; Lichstein, 2007) to examine evidence for mechanisms of geography of synchrony. MRM is a now-standard approach for exploring statistical determinants of quantities describing relationships between sampling locations while taking into account the non-independence of such relationships (Anderson et al., 2017, 2019; Haynes et al., 2013; Walter et al., 2017). MRM evaluates statistical similarities between the spatial structure of plant cover synchrony, represented by a synchrony matrix, and the spatial structure of putative mechanisms. Significant similarity is evidence supporting the putative mechanism as an actual mechanism of the geography of synchrony. We tested whether plant cover synchrony matrices can be explained by spatial proximity, by spatial patterns of gopher disturbance or soil depth, or by interactions with other plant species. Synchrony matrices were developed as described above, and analyses were carried out separately at short and long timescales. Similarity in soil depth was quantified by taking the absolute difference in mean soil depth between site pairs and rescaling the difference d to a similarity according to $1 - [d/\max(d)]$. Spatial proximity was quantified by rescaling the Euclidean distance between sites using the same formula.

We assessed whether these factors explain geography of synchrony in two steps. First, we tested whether the spatial structure of synchrony in each plant species (i.e. its synchrony matrix) was explained by spatial proximity, spatial structure of synchrony in gopher disturbance, and soil depth similarity using MRM containing a single predictor. Second, we tested relationships between the geographies of synchrony of plant species. For the second analysis, we controlled for any predictors from the first analysis that were statistically significant at $\alpha = 0.05$; we then added as a predictor the synchrony matrix for each other plant species, one by one in separate tests. In other words, we tested whether spatial structure in synchrony of each plant species explained that of each other plant species, while controlling for (as necessary) spatial proximity, spatial structure of gopher disturbance synchrony, and soil depth similarity. MRM was implemented using the ECODIST R package (Goslee & Urban, 2017).

2.5 | Analyses: Drivers of site-wide synchrony

We used spatial wavelet coherence (Sheppard et al., 2016) and its extension, multivariate wavelet linear models (Sheppard et al., 2019), to examine drivers of synchrony, including the potential for competition among plant species to drive synchrony across our plots. In contrast to our geography of synchrony analyses, which focused on synchrony between plot pairs, spatial wavelet coherence examines temporal fluctuations shared across all plots, with significant coherence helping determine drivers of synchrony (Sheppard et al., 2016). We compare these results to the MRM results to answer whether drivers of synchrony are the same as mechanisms of geography of synchrony. Although the direction of causation is not revealed by spatial wavelet coherence, it is often clear from the biological circumstances that only one direction is possible. The possibility of a joint effect of an unmeasured variable of course cannot be eliminated. Multivariate wavelet linear models extend coherence testing to account for effects of multiple predictors, analogous to multiple linear regression. Given wavelet transforms of the response and predictor variables for each plot, wavelet multivariate linear modelling finds timescale-specific coefficients maximizing the spatial coherence between the wavelet transforms of the response variable and a linear combination of wavelet transforms of the predictor variables (Sheppard et al., 2019). All the wavelet coherence and linear modelling approaches we used are standard and/or were described precisely by Sheppard et al. (2016, 2019).

Analogous to our MRM models, we began by testing for spatial wavelet coherence between plant cover dynamics and four potential drivers of synchrony: gopher disturbance, PDSI during the growing season, fall precipitation and winter precipitation. We then used multivariate wavelet linear models to test for coherence between plant species, one pair at a time, while controlling for any environmental factors that were significantly coherent with dynamics of the focal plant species at $\alpha = 0.05$. We extracted phase relationships between response and predictor variables to assess the nature of coherence between variables. Phase relationships (φ) are expressed in fractions of π such that $|\varphi| < 0.25$ correspond to approximately in-phase relationships (e.g. positive correlation), $|\varphi| > 0.75$ corresponds to approximately antiphase relationships (e.g. negative correlation) and $0.25 \le |\varphi| \le 0.75$ corresponds to quarter-phase relationships in which fluctuations in one variable lead or lag the other by a fraction of a cycle. Short and long timescales were analysed separately. Like the plant time series, environmental time series were detrended, scaled and normalized prior to analysis.

Significance of wavelet coherence and wavelet linear model effects was tested against $n = 10,000$ Fourier or amplitude-adjusted Fourier transform (AAFT) surrogates that retain spatial and temporal autocorrelation properties of the empirical time series, but have random phase differences and hence can be coherent only by chance (Sheppard et al., 2016). For plant cover variables and climate variables, Fourier surrogates were used; for gopher disturbance time series, AAFT surrogates were used. This was because gopher disturbance time series had too many zeros to be pre-normalized by Box-Cox transformation, and such pre-normalization is necessary to apply Fourier surrogates (Schreiber & Schmitz, 2000). Wavelet methods are implemented in an open-source software package for the R programming language, WSYN (Reuman et al., 2019). Methods and their implementation using 'wsyn' are described in detail in the package VIGNETTE.

3 | RESULTS

3.1 | Micro-geography of synchrony

Over the 33-year time series the abundances of our six focal species fluctuated widely (Figure 2), and for each species, these fluctuations were spatially synchronous (Figure 3). Synchrony of both plant species (Figure 3) and gopher disturbance (Figure 4a) tended to decline with the distance between plots, but with large variation around the median relationship. This variation was partly captured by network modularity, represented by the tendency for synchrony between locations in the same module to be greater than synchrony between locations in different modules (Figures 3 and 4a).

The spatial synchrony networks of all plant species consisted of two to three modules (Figure 5). At short timescales, the networks for all plant species except *Vulpia* ($p = 0.19$) were significantly modular ($p < 0.05$; Table S2), indicating clear subdivision of the site into different sub-groups of locations having relatively high within-group synchrony. Modules often were not geographically compact, with relatively strong synchrony manifesting between even the most distant plots in our study and across treatment blocks (Figures 4c and 5), indicating that distance-decay is not the sole meaningful spatial pattern of synchrony in this system. At long timescales no plant synchrony network was significantly modular. Synchrony in gopher disturbance exhibited apparent modularity (Figure 4c), but modularity could not be significance tested because the time series could not be normalized, making our parametric bootstrapping approach inappropriate. Module groupings were not necessarily similar between short and long timescales, or between species (Figures 4c and 5; Figures S4c and S5). The results of this section answer Q1 in the affirmative, demonstrating a geography of synchrony at this site that occurs on much smaller spatial scales than what has been demonstrated for other systems.

3.2 | Causes of micro-geography of synchrony

Geographies of synchrony in abundant plant species at Jasper Ridge were explained chiefly by spatial proximity and by geographies of

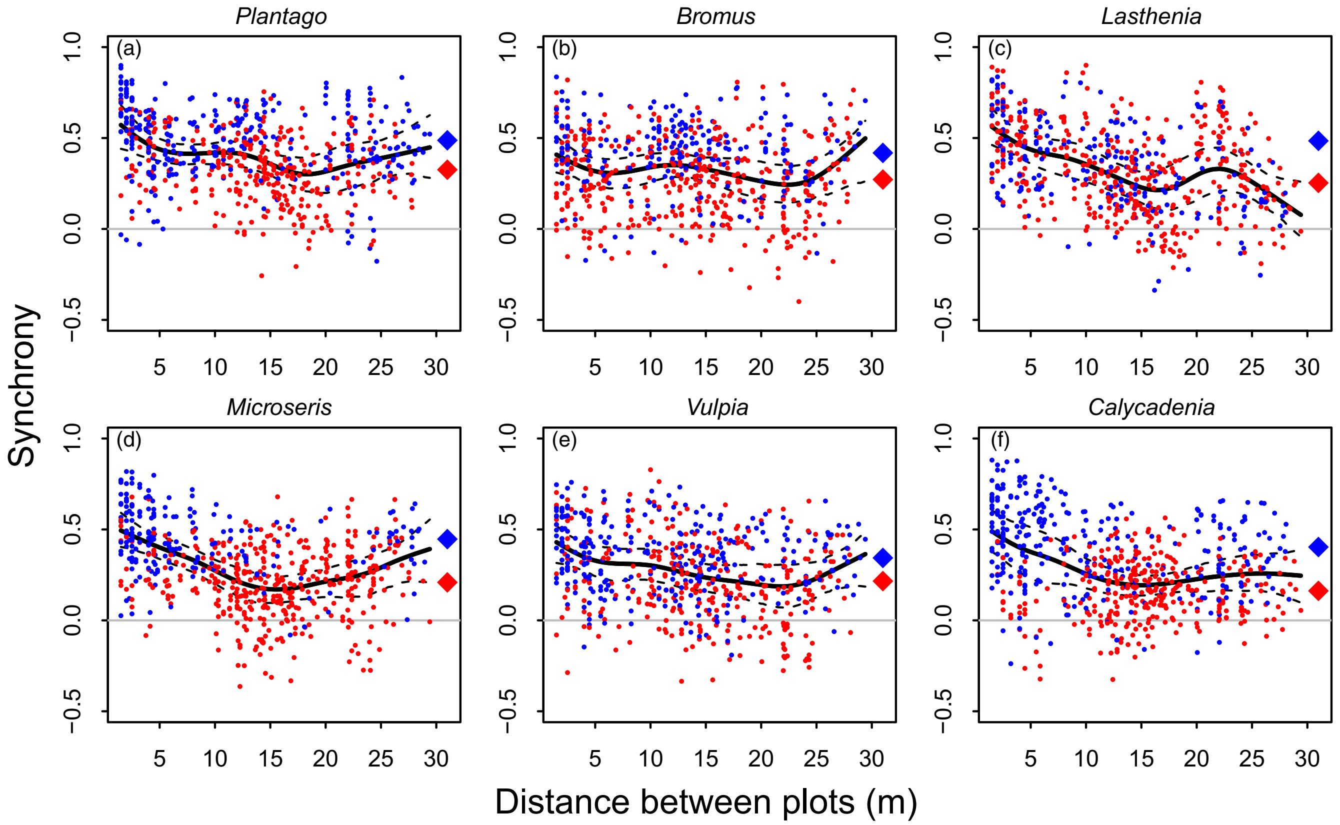

FIGURE 3 Distance decay of synchrony (integrated real part of the cross-wavelet transform, ReXWT; see Section 2) at short timescales (2–6 years) for the focal plant species (a–f). The solid black line indicates the median distance decay, and dashed lines indicate 95% bootstrap confidence intervals. Synchrony between location pairs in the same module is plotted in blue; synchrony between locations in different modules is plotted in red. Dots indicate synchrony between individual plot pairs; diamonds on the right extreme of the plot indicate the means of within- and between-module synchrony. See Figure S3 for long timescales

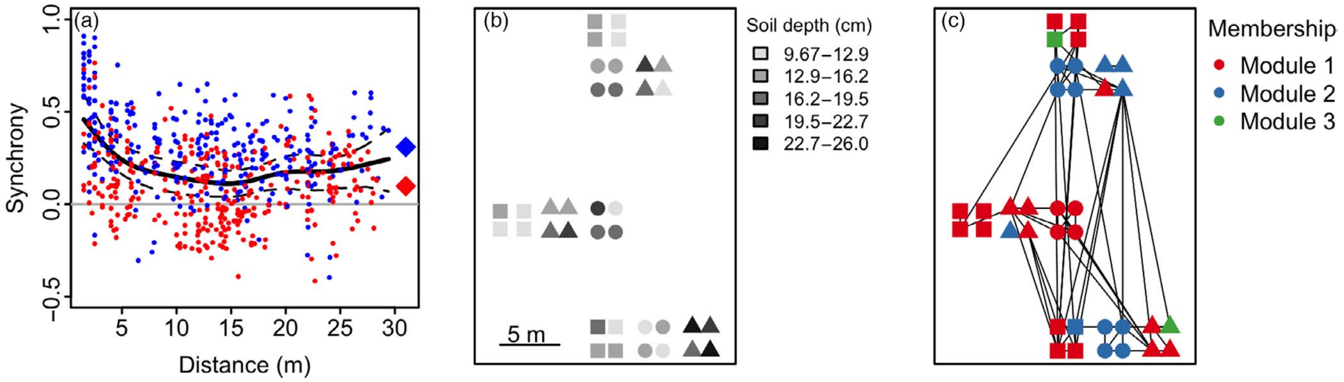

FIGURE 4 (a) Distance-decay in synchrony (integrated real part of the cross-wavelet transform, ReXWT; see Section 2) of gopher disturbance at short timescales (2–6 years). Synchrony between location pairs in the same module is plotted in blue; synchrony between locations in different modules is plotted in red. Dots indicate synchrony between individual plot pairs; diamonds on the right extreme of the plot indicate the means of within- and between-module synchrony. (b) Site map showing locations of plots, experimental treatments, and soil depth. Code to experimental treatments: squares = control; circles = gopher exclosure; triangles = rabbit exclosure. (c) Synchrony network map for gopher disturbance at short timescales with node colours indicating module identity and links between plots indicating the strongest 10% of synchrony relationships (0.49–0.91). Locations of nodes correspond to plot locations. See Figure S4 for long timescales

synchrony in gopher disturbance, with lesser roles for soil depth and interspecific relationships (Q2). Whether these variables were significant explainers of geographies of plant synchrony varied across plant species and depended on timescale. At short timescales, spatial proximity and synchrony in gopher disturbance predicted spatial patterns of short-timescale synchrony in nearly all plant species (Table 1). Despite twofold variation in soil depth across the site (10–26 cm; Figure 4b), soil depth similarity was overall a weaker

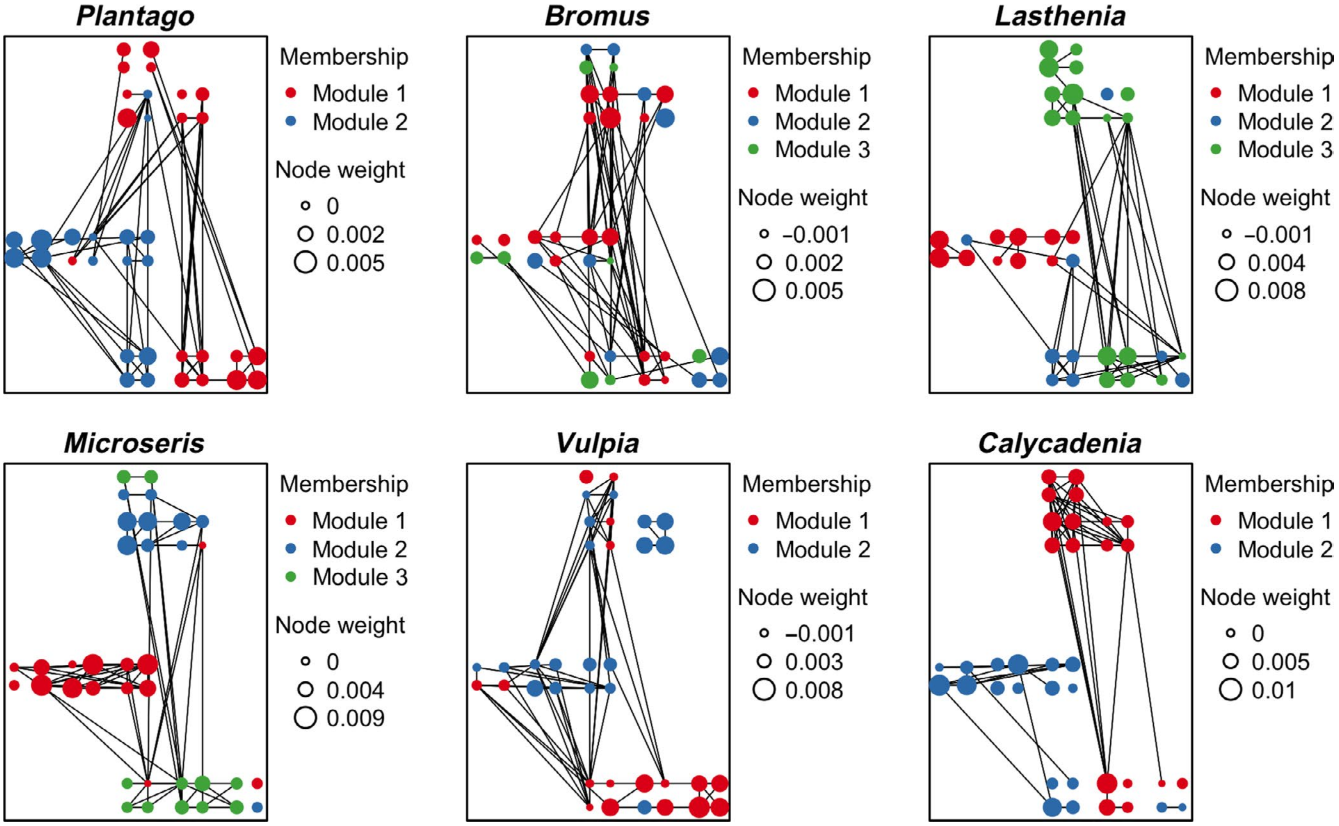

FIGURE 5 Synchrony network maps for short timescales (2–6 years). Node colours indicate module identity. Note that module colours are not related across species. Node shapes correspond to experimental treatments that influenced the frequency of gopher disturbance: squares = control; circles = gopher exclosure; triangles = rabbit exclosure. Only the strongest 10% of links are drawn; these correspond to ranges of the ReXWT: 0.66–0.90 (*Plantago*); 0.58–0.84 (*Bromus*); 0.65–0.90 (*Lasthenia*); 0.57–0.82 (*Microseris*); 0.57–0.83 (*Vulpia*); 0.59–0.88 (*Calycadenia*). Locations of nodes correspond to plot locations. See Figure S5 for long timescales

TABLE 1 MRM coefficients corresponding to effects of: spatial proximity, synchrony in gopher disturbance, similarity in soil depth, and synchrony of interacting plant species. Coefficients for short timescales (2–6 years) appear on top of coefficients for long timescales (>6 years). Stars indicate statistical significance: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Relationships between plants were tested after controlling for other effects that were statistically significant at $\alpha = 0.05$. Key to species abbreviations: PLER = *Plantago erecta*, BRHO = *Bromus hordeaceous*, LACA = *Lasthenia californica*, MIDO = *Microseris douglasii*, VUMI = *Vulpia microstachys*, CAMU = *Calycadenia multiglandulosa*

	PLER	BRHO	LACA	MIDO	VUMI	CAMU
Proximity	0.184*** 0.077*	0.086* 0.098	0.346*** 0.005	0.250*** 0.174***	0.210*** 0.589***	0.225*** 0.065
Gophers	0.294*** 0.069*	0.076 0.019	0.306*** 0.127**	0.214*** 0.076**	0.191*** 0.047	0.222*** 0.046
Soil depth	0.206* 0.073	0.204* 0.090	0.041 0.030	0.025 0.442***	0.081 −0.010	0.044 0.195
PLER	—	0.097 0.344***	0.206** −0.075	0.096 0.034	0.003 −0.162	0.072 0.215
BRHO	0.065 −0.155***	—	−0.117 −0.056	0.062 −0.022	0.057 −0.047	−0.048 0.107
LACA	0.168** −0.028	−0.104 −0.042	—	0.095 0.095	−0.057 −0.165	0.137* 0.005
MIDO	0.075 0.058	0.069 0.022	0.101 0.210	—	−0.055 −0.065	0.097 0.380**
VUMI	−0.007 −0.032	0.057 0.001	−0.056 −0.081	−0.051 −0.007	—	0.085 0.035
CAMU	0.053 0.086	−0.035 0.101	0.129* −0.009	0.087 0.140*	0.083 0.557	—

predictor of geographies of synchrony, although it was statistically significant for the two most abundant species, *P. erecta* and *Bromus hordeaceous*. Geographies of synchrony were positively associated between the *Plantago* × *Lasthenia* and *Lasthenia* × *Calycadenia* species pairs. On long timescales, spatial proximity and gopher disturbance synchrony were generally also the most important predictors of geographies of plant synchrony (Table 1), but were less strongly and consistently related to geographies of plant synchrony than was the case at short timescales. Notable differences between short and long timescales were observed for *Microseris*, which had a strong, positive relationship with soil depth similarity at long timescales, but no significant relationship at short timescales. There were long-timescale relationships between geographies of synchrony for the *Plantago* × *Bromus* and *Microseris* × *Calycadenia* species pairs.

3.3 | Drivers of site-wide synchrony and how they connect to the geography of synchrony

Spatial wavelet coherences supported gopher disturbance as a driver of short-timescale synchrony across the entire site (Table 2). On short timescales, *Plantago*, *Lasthenia* and *Calycadenia* exhibited significant, approximately anti-phase responses to gopher disturbance; that is, gopher disturbance reduced plant cover. Moran effects likely also drove spatially synchronous fluctuations in plant cover, and we identified short-timescale climate drivers of site-wide synchrony for *Plantago*, *Microseris* and *Calycadenia* (Table 2). Interestingly, these relationships ranged from approximately in-phase to quarter-cycle to approximately anti-phase, suggesting the potential for diverse responses of plant species to environmental drivers (i.e. compensatory dynamics) to partially buffer community-aggregate plant productivity. Neither gopher disturbance nor any climatic variables were significantly coherent with any plant species at a site-wide level at long timescales (Table 2).

Some pairs of plant species were significantly coherent across the entire site after controlling for significant environmental factors using wavelet linear models. On short timescales (<6 years), *Vulpia* dynamics were significantly coherent with fluctuations in *Plantago*, *Bromus*, *Lasthenia* and *Microseris* (Table 2). These relationships were approximately in-phase, except for a quarter-cycle relationship between *Plantago* and *Vulpia*. At long timescales, *Plantago* and *Bromus* were related in antiphase, *Plantago* and *Microseris* were coherent with a quarter-cycle phase shift, and *Bromus* and *Microseris* also had a quarter-cycle relationship (Table 2). Note that type-1 error rates at $\alpha = 0.05$ indicate that, for the number of tests we performed, assuming independent tests, we could observe three apparently statistically significant relationships between plants due to chance. Consequently, the significance of plant-plant coherence results may have been marginal after accounting for multiple testing.

These results help answer the part of Q2 concerning whether mechanisms of the geography of synchrony were related to mechanisms of synchrony: the fact that gophers were implicated in both

TABLE 2 Phase relationships (as fractions of π) for coherences with gopher disturbance, growing season PDSI, fall precipitation, winter precipitation, and other plant species. Stars indicate statistical significance of the magnitude spatial wavelet coherence: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Results for short timescales are given on top of results for long timescales. Coherences among plants were tested after controlling for any gopher or climate effects that were statistically significant at $\alpha = 0.05$. Phase angles (φ) are reported in fractions of π such that $-0.25 < \varphi < 0.25$ correspond to approximately in-phase relationships, $|\varphi| > 0.75$ corresponds to approximately antiphase relationships, and $0.25 \le |\varphi| \le 0.75$ corresponds to quarter-phase relationships in which fluctuations in one variable lead or lag the other by a fraction of a cycle. Negative phases indicate that the response variable lags (peaks after) the predictor variable. Key to species abbreviations: PLER = *Plantago erecta*, BRHO = *Bromus hordeaceous*, LACA = *Lasthenia californica*, MIDO = *Microseris douglasii*, VUMI = *Vulpia microstachys*, CAMU = *Calycadenia multiglandulosa*

	PLER	BRHO	LACA	MIDO	VUMI	CAMU
Gophers	−0.952*** −0.996	0.091 0.084	−0.817*** 0.031	−0.710 −0.165	−0.193 −0.148	−0.901*** 0.961
PDSI	0.570* 0.990	−0.563 −0.167	0.075 0.509	0.215*** 0.334	0.078 0.170	0.824* −0.367
Fall prcp.	0.149 0.282	0.732 −0.630	−0.856 −0.875	−0.165 −0.837	0.598 0.942	−0.901 0.318
Wint. prcp.	0.089* −0.840	0.928 0.086	−0.016 0.697	0.276 0.487	0.474 0.427	0.694 −0.200
PLER	—	0.793 0.942**	0.166 −0.904	−0.072 0.716	0.413 0.764	0.271 0.158
BRHO	−0.793 −0.942	—	0.764 0.653	0.738 0.500	−0.028 0.192	0.611 −0.290
LACA	−0.166 0.904	−0.764 −0.653	—	0.097 −0.112	−0.005 −0.254	0.303 −0.840
MIDO	0.088 0.716*	−0.742 −0.500*	−0.098 0.112	—	−0.159 −0.346	−0.094 −0.891
VUMI	−0.414* −0.764	0.028* −0.192	0.005* 0.254	0.159** 0.346	—	0.751 −0.531
CAMU	−0.271 −0.158	−0.613 0.290	−0.303 0.840	0.094 0.891	−0.751 0.531	—

our spatial coherence and our MRM analyses suggests that gopher disturbance drives site-wide synchrony, as well as shaping its geography. Relationships between pairs of plant species in both the spatial coherence and MRM analyses suggest that interspecific interactions can both drive synchrony and modify its spatial structure, but the same pairs of species were not related in both analyses, suggesting multiple mechanisms were at play. Soil depth was associated with the geography of synchrony for some species, but could not have caused synchrony itself because it is not a temporally dynamic variable; thus, soil depth contributed to the geography of synchrony, selectively modifying synchrony between some pairs of locations.

4 | DISCUSSION

Spatial synchrony is a pervasive phenomenon, and determining the factors that drive and disrupt synchrony has important implications for understanding population and community stability. Here we demonstrated that geographies of synchrony can manifest at a micro scale, within a single 30-m diameter area of serpentine grassland (Q1). For each plant species, distinct modules of locations exhibited high within-group but low between-group synchrony, and the spatial arrangement of group membership differed across species. This spatial structure was largely shaped by gopher disturbance and dispersal limitation, and somewhat by interactions with other plant species. Gopher disturbance was also implicated as a likely cause of site-wide synchrony, so drivers of synchrony and the geography of synchrony were closely related in this system (Q2).

Despite the importance of spatial proximity, relatively well-synchronized populations were often geographically separate (Figures 3–5). In our study, gopher disturbance occurred unevenly across the landscape and emerged as a primary cause of geographic patterns in synchrony (Q2) for all species but *Bromus*. Gopher disturbances were patchy and episodic, but some patches tended to have more similar disturbance histories than others, and hence had more synchronous plant dynamics. Gopher disturbance had a larger influence on plant species' geographies of synchrony at short than long timescales. This may reflect the life history of plants in an annually dominated community with small-scale disturbances. While the immediate effects of disturbance will result in a population decline, annuals can recover quickly and may on average benefit from disturbance, as patches can reach pre-disturbance stem densities within 2 years (Hallett et al., 2018).

Our spatial coherence results indicate that gopher disturbance was a driver of spatial synchrony in plant dynamics. However, gopher disturbance was itself less spatially synchronous than were plant dynamics (compare Figures 3 and 4a), which is unusual since drivers of spatial synchrony are often more synchronous than population dynamics (Liebhold et al., 2004). Because our study area is only 30 m across, the contribution of weather to plant synchrony must be very high. Since the synchrony of gopher disturbance was much lower, gopher disturbance likely reduced plant spatial synchrony from its expected strength if dynamics were driven by weather alone. Gopher disturbance can still be implicated as a cause of synchrony in the sense that it shaped the nature of synchrony, and in the sense that plant spatial synchrony was higher than it would have been if gopher disturbance time series were completely asynchronous across plots. The same kind of mechanism of synchrony was shown to occur for a phytoplankton density index (PCI) in the seas around the UK: PCI synchrony was lower than it would have been absent the influence of a copepod consumer *Calanus finmarchicus*, but was higher than it would have been if *C. finmarchicus* dynamics were themselves totally spatially asynchronous (Sheppard et al., 2019).

We are now in a position to conceptually connect the micro-geographies of synchrony in this system with questions of ecological stability (Q3). Factors which introduce geographies of synchrony may be expected to have a positive effect on a species' overall stability by reducing synchrony between some groups of plots, and thereby reducing the variability of its total abundance across all plots. Our results indicate that gopher disturbance probably fills this role in our grassland system. Reductions in synchrony theoretically promote metapopulation persistence (Heino et al., 1997) and potentially stabilized fluctuations in spatially aggregated species abundances size across our site. Our result that micro-geographies of synchrony can occur on spatial scales as small as 30 m, a scale on which non-spatial approaches to population and community ecology are often practiced, is particularly notable because it means micro-geographies of synchrony may be a heretofore unappreciated mechanism of stability at both the population and community levels of ecology.

Community synchrony also has previously well-understood implications for stability at the community level of organization, but the mechanisms operating in that context are distinct from the mechanism we suggest involving micro-geographies of synchrony. For instance, differences in species' recovery rates to disturbance are known to help maintain diversity and stabilize productivity across plots with different disturbance histories. Episodic local disturbances can maintain diversity in a system with an underlying competitive hierarchy (Hobbs & Huenneke, 1992; Hobbs & Mooney, 1995). The temporally lagged recovery of subdominant plant taxa from disturbance manifests as a form of compensatory dynamics that contributes to stabilization of aggregate primary productivity (Brown et al., 2016; Gonzalez & Loreau, 2009). These mechanisms are distinct from the micro-geographic mechanism described above because they involve compensatory dynamics between species, rather than compensation in the dynamics of the same species as it occurs in different plots across a site. The observation that geography of synchrony holds at smaller spatial scales is a strong reminder that a meaningful scale of study depends on the interplay between biotic interactions and spatial heterogeneity (e.g. Pearson & Dawson, 2003; Vivian-Smith, 1997), which can inform questions of stability in both population and community ecology.

Our serpentine grassland system may or may not be atypically susceptible to micro-geographies of synchrony; additional small-spatial-scale studies of the geography of synchrony are necessary to determine to what extent micro-geographies may be common and the potential mechanisms described above may be important for classical population and community ecology. On one hand, the modest dispersal ranges (1 m maximum; Hobbs & Mooney, 1985) of the plant species in our study suggest an intrinsic propensity for small-scale geographies of synchrony. On the other hand, many systems may be subject to disturbances on scales similar to the gopher disturbances of this study, and such disturbances could produce micro-geographies of synchrony in other systems as they did here.

Most prior research on how interspecific interactions shape spatial synchrony has focused on predator-prey or host-parasitoid systems (Liebhold et al., 2004). We found some evidence that within-guild dynamics can shape spatial synchrony. Considering short and long timescales together, four pairs of species had significantly related geographies of synchrony (Table 1). Additionally, the four most abundant plant species all had coherent dynamics with *Vulpia* at short timescales, and three species pairs exhibited coherent dynamics at long timescales (Table 2). *Vulpia* has a wide distribution across gradients of environmental stress but is subject to strong competitive effects in less stressful conditions (Jurjavcic, Harrison, & Wolf, 2002). As such, its synchrony patterns may be largely driven by the synchronous oscillations of its competitors. For example, after controlling for the effects of weather and gopher disturbance, changes in *Vulpia* cover lagged changes in *Plantago* cover, suggesting a response of the sub-dominant species to changes in the abundance of the dominant competitor.

Indeed, most significant interspecific relationships across both MRM and coherence analyses involved the dominant competitor *Plantago*. This suggests that when interspecific interactions shape synchrony, it is often due to a cascading effect of dominant species on subdominants in the community. However, relationships among plant species were less common and tended to be weaker than effects of gopher disturbance and precipitation, suggesting that interspecific competition is the less important of these factors. This may be because serpentine grasslands are characterized by niche differentiation (Levine & HilleRisLambers, 2009) and minimal niche overlap (Hallett et al., 2018). In systems characterized by either pronounced competitive or facilitative dynamics, we might expect within-guild interspecific interactions to have a strong effect on the structure of population spatial synchrony. Notably, the only non-native focal species, *B. hordeaceous*, differed from native species by exhibiting minimal distance-decay in synchrony and neither its geography nor temporal dynamics were related to gopher disturbance. Exploring the response and interspecific effect of invading species on synchrony dynamics is another potentially interesting avenue to explore.

Further conceptual and methodological integration of population and community synchrony stands to improve understanding of the ecology of these systems and consequences for ecosystem stability. In our study, micro-scale geographies of population spatial synchrony created a spatial structure in which different networks were independent or asynchronous from each other over time. There is a growing recognition of the importance of spatial heterogeneity in community stability (Wang et al., 2019; Wang & Loreau, 2014; Wilcox et al., 2017); exploring factors that structure geographies of synchrony may provide insights into the mechanisms that underlie these patterns. We also found empirical evidence supporting a role of competition in determining site-wide synchrony and its spatial structure, which is generally consistent with recent theory on population and interspecific synchrony among competitors (Jarillo, Saether, Engen, & Cao, 2018; Lee, Saether, & Engen, 2019). Studies of synchrony offer a natural approach given the recognized importance of synchrony in population and community ecology, and that many statistical approaches are applicable to both cases.

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AUTHORS' CONTRIBUTIONS

R.J.H. and L.M.H. collected the data; J.A.W., L.M.H., L.W.S., L.Z., K.N.S. and D.C.R. conceived the study; J.A.W., L.W.S., L.Z., T.L.A. and D.C.R. developed methods and associated analysis code; J.A.W. conducted the analyses; J.A.W. and L.M.H. drafted the manuscript. All authors contributed substantially to revisions of the manuscript and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and analysis code reproducing the results of this paper have been archived in an Environmental Data Initiative (EDI) repository and are available at https://doi.org/10.6073/pasta/b34798fd71e24efd3fda995ec4263701 (Hallett et al., 2020).

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