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Drivers of synchrony of acorn production in the valley oak (*Quercus lobata*) at two spatial scales

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Abstract. We investigated spatial synchrony of acorn production by valley oaks (*Quercus lobata*) among individual trees at the within-population, local level and at the among-population, statewide level spanning the geographic range of the species. At the local level, the main drivers of spatial synchrony were water availability and flowering phenology of individual trees, while proximity, temperature differences between trees, and genetic similarity failed to explain a significant proportion of variance in spatial synchrony. At the statewide level, annual rainfall was the primary driver, while proximity was significant by itself but not when controlling for rainfall; genetic similarity was again not significant. These results support the hypothesis that environmental factors, the Moran effect, are key drivers of spatial synchrony in acorn production at both small and large geographic scales. The specific environmental factors differed depending on the geographic scale, but were in both cases related to water availability. In addition, flowering phenology, potentially affecting either density-independent pollination failure (the pollination Moran effect) or density-dependent pollination efficiency (pollen coupling), plays a key role in driving spatial synchrony at the local geographic scale.

Key words: acorn production; masting; Moran effect; phenology; Quercus lobata; *spatial synchrony.*

Introduction

The mechanisms driving spatial synchrony, the tendency for the size or density of spatially disjunct populations to correlate through time, is a subject of debate despite the ubiquity of this phenomenon (Liebhold et al. 2004*a*). In the case of variable and synchronized seed production known as masting behavior, two processes stand out as being potentially critical to what has in many cases been found to be widespread spatial synchrony both geographically (Koenig and Knops 2013) and interspecifically (Schauber et al. 2002): the Moran effect, whereby populations with identical density-dependent dynamics display the same degree of synchrony as environmental factors, typically weather (Moran 1953, Ranta et al. 1997), and enhanced pollination efficiency or "pollen coupling," particularly in wind-pollinated species (Kelly et al. 2001, Kelly and Sork 2002).

The first of these processes is almost always potentially significant given that both temperature and precipitation exhibit geographically widespread spatial synchrony, often up to distances of 1,000+ km, across all continents (Koenig 2002). The second, pollen coupling, is a form of dispersal that has the potential to drive synchrony by means of phase locking among populations of wind-pollinated, obligate outcrossing species far more distant than the scale of local dispersal (Ranta et al. 1998, Satake and Iwasa 2000, 2002).

There are several additional factors that may influence spatial synchrony of seed production. One is flowering phenology, which potentially affects both density-dependent pollination efficiency (pollen coupling) and density independent pollination failure (pollination Moran effect; Pearse et al. 2016). The latter is expected to be driven primarily by a mechanistic response to weather (Pearse et al. 2014), and since previous work has demonstrated a strong relationship between weather and phenology in this population (Koenig et al. 2012, 2015), it is likely that a pollination Moran effect is in play and that flowering phenology has a strong effect on spatial synchrony.

In addition, numerous other variables are potential drivers of spatial synchrony in masting species but have not been previously examined. Among these are genetic similarity, which may be important at all spatial scales to the extent that the investment in, and timing of, seed production by individual trees is under genetic control. Second are landscape features differing in their "resistance" to pollen dispersal, which may significantly interfere with gene flow in ways that ultimately affect ecological factors such as synchrony of seed production (Grivet et al. 2006, Sork et al. 2010, Gharehaghaji et al. 2017). A third class of factors consist of edaphic and other local environmental conditions, which may be

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important at local spatial scales where they can potentially mask the synchronizing influence of the Moran effect (Peltonen et al. 2002).

Previous work has shown that spatial synchrony in acorn production by the valley oak (*Quercus lobata*) encompasses its entire geographic range, consistent with the hypothesis that the Moran effect is a key driver of synchrony (Koenig and Knops 2013). Here we expand these earlier results, employing multiple regression on distance matrices (MRMs) to estimate the relative importance of different drivers of spatial synchrony in seed production (Manly 1986, Lichstein 2007, Haynes et al. 2013) including geography (Euclidean distance and an estimate of habitat resistance based on land cover type), environmental factors (weather, water availability, and soil nutrients), flowering phenology, and genetic similarity. In addition to employing this relatively new statistical methodology and testing several previously unexplored factors as potential drivers of synchrony, we conduct analyses at two complementary spatial scales: among individuals within a single population (the local scale), and among populations across the geographic range of the species (the statewide scale). Although it was not possible to measure the same exact variables at both scales in all cases, we are still able to compare the relative importance of different categories of variables.

Methods

Species and study sites

To examine spatial synchrony in acorn production at the statewide scale, we estimated annual seed production on 250 individually tagged *Q. lobata* distributed across its range as part of the California Acorn Survey. Analyses at the local scale were conducted on a sample of 86 trees at Hastings Reservation in central coastal California, near the middle of the range of *Q. lobata*, for which we quantified acorn production over a 37-yr period (1980–2016; Koenig et al. 1994*b*). In addition, we estimated acorn production on 164 trees at nine additional sites spread across the range of *Q. lobata* except for the Central Valley and the Santa Monica Mountains (Appendix S1: Fig. S1). The time period over which data were taken at these sites varied (Appendix S1: Table S1), ranging from 2008–2016 (9 yr) to 1989–2016 (28 yr).

Quercus lobata is a "white" oak in the section *Quercus* that matures acorns in a single season, is a California endemic, and is distributed throughout the foothills ringing the Central Valley (Appendix S1: Fig. S1) up to about 1800 m elevation (Griffin and Critchfield 1972). Within its total estimated range of 1,967 km^2 (Bolsinger 1988), *Q. lobata* stands often consist of relatively few, often very large, trees.

The acorn crop on each tree was estimated each year by means of visual surveys in which two observers scanned different parts of the canopy and counted as many acorns as they could in 15 s (Koenig et al. 1994*a*). Summed counts were ln-transformed (ln[acorns counted in 30 s + 1] = LN30) to reduce non-normality. For site means, we averaged the ln-transformed values across all individuals.

Additional data were available for the Hastings Reservation trees only. This included mean budburst date estimated from weekly phenology surveys conducted from 2003 to 2016 during which we determined, for each tree, the Julian date of budburst defined as the first date on which at least 5% of the tree had leafed out and was green (Koenig et al. 2015); soil nitrogen and phosphorus availability estimated by four ion-exchange resin bags placed under each tree at a depth of 5–10 cm between October 1992 and April 1993 (Knops and Koenig 1997); and an estimate of water availability based on predawn xylem water potential (XWP) measured using a pressure bomb in September 1991 and 1994–1998 (Knops and Koenig 1994, Barringer et al. 2013). XWP varies depending on rainfall, but differences among trees are concordant among years (Knops and Koenig 2000), and thus we restricted our analyses to data collected in 1991, when all trees were measured.

Landscape data

We determined the Euclidean distance (proximity) between all pairs of sites at the statewide scale and all pairs of trees at the local scale. In addition, at the statewide scale we tested an index of habitat resistance based on land cover type. The rationale for this latter analysis was that habitat connectivity affects pollen flow insofar as particular habitats such as coniferous forests reflect physical barriers such as mountains. Thus, to the extent that pollination efficiency is important to patterns of seed production in the short term or gene flow is important in the long-term, habitat resistance is potentially a more important driver of spatial synchrony of seed production than physical distance. Details for the model generating the values used here (which was the model with the most support based on Circuitscape 4.0.5 [McRae et al. 2013]) are provided by Gharehaghaji et al. (2017).

Molecular data

Patterns of genetic similarity at neutral loci, which are a consequence of long-term historical processes, test the potential role of genetic similarity as a driver of patterns of seed production. Statewide analyses were based on eight microsatellite loci derived from 14–26 individuals collected at each of the 10 localities (Appendix S1: Table S1); details are provided in Ashley et al. (2015). For the Hastings site analyses, we used six of these microsatellite loci derived from 82 of the trees for which we had both acorn production and molecular data; for further details see Abraham et al. (2011).

For the statewide data, we tested two measures of genetic differentiation: the *F* statistics analogues Θ (Weir and Cockerham 1984) and the more recently derived

D_{JOST} (Jost 2008). Results were unchanged regardless of which measure or combination of measures was used, so we report only results for $D_{JOST.}$ Values were from Ashley et al. (2015: Table 1). For the Hastings site analyses, we used pairwise genetic relatedness calculated using GenAlEx 6.5 (Peakall and Smouse 2006, 2012).

Weather variables

Acorn production by *Q. lobata* is strongly correlated with mean maximum April temperatures (Koenig et al. 2015). Consequently, we restricted the local analyses to mean maximum April and mean annual temperature. For the statewide analyses, we used mean maximum April temperature, mean annual temperature, and annual rainfall where annual values were measured (for year *x*) from 1 September of year $x - 1$ to 31 August of year *x*. Because of limitations of the temperature recorders, annual values for the local data were measured from 1 November of year $x - 1$ to 31 August of year *x*.

Statewide weather data was derived from the PRISM climate group (Oregon State University, Corvallis, Oregon, USA) matched geographically to the sites. For the individual tree analyses at Hastings Reservation, we used mean maximum April temperature at each tree obtained from small automated temperature recorders (iButtons; Maxim Integrated Products, Sunnyvale, California, USA) located on the north side of trees approximately 1.5 m above ground programmed to record temperatures at 4-h intervals starting at 04:00 each day. Temperature patterns measured in this manner have previously been shown to vary in ways that potentially drive variation in annual acorn production in this population (Koenig et al. 2015). iButtons were first deployed in 2004 and provided data for all trees starting in 2009.

Analyses

All analyses were conducted in R 3.3.1 (R Development Core Team 2016). For variables that consisted of annual values, including acorn production, weather, and flowering phenology, we calculated the pairwise correlation coefficients between annual values of individual trees for the local analyses and between annual site means for the statewide analyses. For distance variables (calculated using the dist function in the R library fields [Nychka et al. 2015]), values were converted to indices of similarity by the formula [1 – (measure of distance/maximum distance)] (Haynes et al. 2013).

For the local analyses, sample sizes for acorn production, flowering phenology, and temperature allowed visualization of spatial synchrony using the nonparametric covariance functions (Bjørnstad and Falck 2001) of the R library ncf (Bjørnstad 2013), which tests for declines with distance using Mantel tests. Spatial synchrony of acorn production and weather at the statewide scale, for which the number of sites was too small for analysis using nonparametric covariance functions, was quantified using the modified correlogram method (Koenig and Knops 1998).

In order to determine the relative importance of multiple factors as potential drivers of spatial synchrony, we performed multiple regression on distance matrices analyses using the program MRM in the R library ecodist (Goslee and Urban 2007). Models were chosen to examine the importance of factors within each of the classes of available variables along with saturated models that included all variables. For the analyses within the local population, we performed six sets of analyses: (1) proximity (Euclidean distance); (2) temperature (both mean maximum April temperature and mean annual temperature); (3) environmental variables (xylem water potential, soil nitrogen availability, and soil phosphorus availability); (4) phenology (mean budburst date); (5) genetics (pairwise genetic relatedness); and (6) a saturated model including all variables. For analyses at the statewide scale, we performed four sets of analyses: (1) proximity (Euclidean distance and habitat resistance based on landscape features); (2) weather (mean maximum April temperature, mean annual temperature, and annual rainfall); (3) genetics (D_{JOST}); and (4) a saturated model including all variables (with the exception of habitat resistance, which failed to outperform the more straightforward measure of Euclidean distance). As stated above, all "distance" variables were converted to similarity indices. For each factor in each MRM analysis, we list the coefficient of the effect size, the variable's P value, the R^2 of the model, and the P value of the model determined from 1,000 permutations of the data.

Results

Patterns of spatial synchrony

As found in prior studies, spatial synchrony in acorn production was significantly greater than zero across all distances at both the local (Liebhold et al. 2004*b*) and statewide (Koenig and Knops 2013) scales (Fig. 1; Appendix S1: Fig. S2; Appendix S1: Table S2). Synchrony was also highly significant across the entire spatial scale for flowering phenology at the local scale (Appendix S1: Fig. S3) and for all weather variables, both at the statewide (Appendix S1: Tables S3–S5) and local scales (Appendix S1: Figs. S4–S5).

There were, however, differences in the pattern of decline observed in spatial synchrony with distance. At the local scale, synchrony declined (correlations with distance were all negative) for all variables (Appendix S1: Figs. S2–S5) but the declines were small and either barely significant ($P = 0.03$ for phenology) or not significant ($P > 0.05$ for acorn production and the weather variables) based on Mantel tests. At the statewide scale, the decline in spatial synchrony of acorn production was more or less linear (mean *r* for the three increasing distance categories was 0.528, 0.495, and 0.370; Appendix S1: Table S2) whereas for the weather

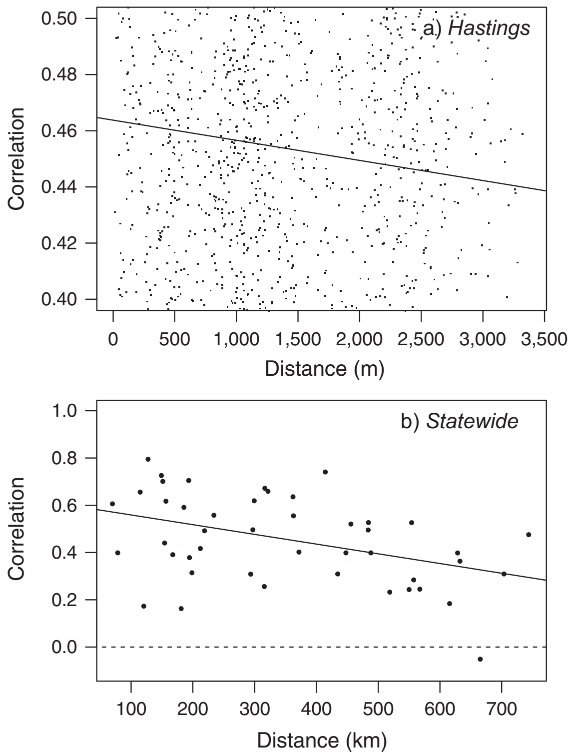

FIG. 1. Spatial synchrony of acorn production by (a) individual trees (n = 86) at the local level (regression of mean pairwise correlations on distance, $r = -7.16 \times 10^{-6} \times$ distance + 0.464; for statistics, see Appendix S1: Fig. S2); and (b) site means (n = 10) at the statewide level (regression of mean pairwise correlations on distance, $r = -4.11 \times 10^{-4} \times$ distance + 0.600; for statistics, see Appendix S1: Table S2). Each point is a pairwise correlation; the solid line is the regression. Note the difference in the x-axis scales.

variables (Appendix S1: Tables S3–S5) synchrony was greater but did not necessarily decline with distance. For example, mean r for the three increasing distance categories for mean maximum annual temperature was 0.784, 0.655, and 0.707 (Appendix S1: Table S4).

Drivers of spatial synchrony

At the local scale, models including proximity, temperature, and genetic similarity between trees each explained <1% of variance (based on R^2 values) in synchrony of acorn production among trees (Table 1). In contrast, the factors that correlated significantly with spatial synchrony were local environmental factors, primarily water availability, and flowering phenology, with models including these factors each explaining 13.9% of the total variance. These two variables remained highly significant in the saturated model.

At the statewide scale, significant variance in spatial synchrony of acorn production was explained by models including space (both proximity and habitat resistance) and weather (primarily annual rainfall), with the model including genetic similarity again failing to explain a significant proportion of variance (Table 2). Since our estimate of habitat resistance failed to outperform the more straightforward measure of Euclidean distance, we only used the latter variable in the saturated model.

The R^2 values in Tables 1 and 2 compare the proportion of total variance in spatial synchrony of acorn production explained by the different factors at the two spatial scales. At the local scale, the key variables were local environmental factors (water availability) and flowering phenology, with the saturated model explaining 22.2% of variance. At the statewide scale, the model including weather (annual rainfall) explained the largest proportion of variance followed by the model with proximity between sites. The significance of this latter variable, however, was indirect through its relationship with rainfall as indicated by the saturated model, where proximity was no longer significant. In combination, the saturated model explained 40.2% of the variance in spatial synchrony in acorn production observed between sites.

DISCUSSION

These analyses offer several insights regarding the drivers of spatial synchrony in acorn production in the valley oak *Quercus lobata,* a masting tree species that exhibits highly significant spatial synchrony. At the local scale, spatial synchrony of acorn production was primarily explained by individual differences in flowering phenology and differences in water availability between trees. Variables that were not significant included proximity, temperature differences between trees, and pairwise genetic similarity.

A significant effect of phenology on within-population spatial synchrony was previously predicted by studies of this population demonstrating the existence of stabilizing selection for within-season flowering phenology (Koenig et al. 2012). Interpreting the significance of this result is difficult, since it could be indicative of either density-dependent pollination efficiency (pollen coupling) or density-independent pollination failure (pollination Moran effect; Pearse et al. 2016). The latter phenomenon is particularly likely given the strong relationship between microgeographic weather and phenology found in this population (Koenig et al. 2012, 2015). However, the fact that phenology remained significant after controlling for temperature differences between trees (Table 1) suggests that pollen coupling may also be an important driver of synchrony in seed production at this local spatial scale.

At the statewide geographic scale, weather, primarily annual rainfall, which exhibits strong spatial synchrony at near-continental scales (Koenig 2002), explained 37.4% of the total variance in spatial synchrony of mean acorn production between sites. As in the local-scale analyses, genetic similarity was again not a significant predictor of spatial synchrony. Distance between sites and our estimate of habitat resistance based on land cover types were significant by themselves, but not when controlling for annual rainfall in the saturated model.

Table 1. MRM results for spatial, environmental, and genetic factors affecting mean synchrony of *Quercus lobata* seed production at the local level within Hastings Reservation.

Model and variables	Coefficient	*P* (variable)	R^2 (model)	*P* (model)
1. Space			0.001	0.420
Proximity	0.022	0.42		
2. Weather			0.007	0.300
Mean maximum April temperature	−0.100	0.60		
Mean annual temperature	0.067	0.19		
3. Environment (water availability and soil nutrients)			0.139	**0.001**
Xylem water potential	0.426	**0.001**		
Available nitrogen	−0.050	0.34		
Available phosphorus	0.017	0.78		
4. Phenology			0.139	**0.001**
Mean budburst date	0.446	**0.001**		
5. Genetics			<0.001	0.220
Pairwise relatedness	0.047	0.22		
6. Saturated model			0.222	**0.001**
Proximity	−0.022	0.37		
Mean maximum April temperature	−0.212	0.35		
Mean annual temperature	0.102	0.19		
Xylem water potential	0.336	**0.002**		
Available nitrogen	−0.061	0.23		
Available phosphorus	0.009	0.88		
Mean budburst date	0.367	**0.001**		
Pairwise relatedness	0.043	0.20		

Notes: Sample size is n = 81 trees. Values analyzed are correlations except for proximity, soil nutrients, xylem water potential, and genetics, which are distances. Statistically significant values based on 1,000 randomizations (P < 0.05) are in boldface type.

The fact that habitat resistance failed to outperform Euclidean distance suggests that land cover type does not affect patterns of spatial synchrony in acorn production significantly more than physical distance.

Two limitations of our study are worth noting. First, our analyses were limited both by including only a small number of microsatellite loci and by lack of acorn data from the Santa Monica Mountains, the most genetically distinct population identified in this species (Grivet et al. 2008, Ashley et al. 2015, Gharehaghaji et al. 2017). Second was the lack of data on phenological differences among sites or for differences in environmental

Table 2. Multiple regression on distance matrices (MRM) results for spatial, environmental, and genetic factors affecting mean synchrony of *Quercus lobata* seed production for 10 populations at the statewide level across California.

Models and variables	Coefficient	*P* (variable)	R^2 (model)	*P* (model)
1a. Space			0.227	**0.001**
Proximity	0.357	**0.001**		
1b. Space			0.125	**0.013**
Habitat resistance	0.464	**0.013**		
2. Weather			0.374	**0.014**
Mean maximum April temperature	0.387	0.45		
Mean annual temperature	−0.174	0.54		
Annual rainfall	0.784	**0.003**		
3. Genetics			0.058	0.22
D_{JOST}	−0.172	0.22		
4. Saturated model			0.402	**0.021**
Proximity	0.079	0.60		
Mean maximum April temperature	0.192	0.71		
Mean annual temperature	−0.114	0.73		
Annual rainfall	0.695	**0.03**		
D_{JOST}	−0.115	0.27		

Notes: Values analyzed are correlations or distances converted to similarities (proximity and D_{JOST} [Jost 2008]); thus, in all cases more similar sites have higher coefficients. The "saturated" model includes all variables except "habitat resistance," which was considered to be duplicative of proximity (but not as statistically powerful). Statistically significant values (P < 0.05) are in boldface type.

factors comparable to those measured at the local scale other than temperature. Nonetheless, the results at the two spatial scales provide a unique comparison. In both cases, water availability, represented by xylem water potential at the local scale and rainfall at the statewide scale, played a key role in driving spatial synchrony, while genetic similarity and distance between sites were not significant, at least after controlling for weather.

Previous work concluded, based on the very small decline in synchrony with distance observed in *Q. lobata* acorn production at Hastings Reservation (Fig. 1a), that the pattern of spatial synchrony was consistent with the combined effects of the Moran effect and some endogenous factor related to pollination (Liebhold et al. 2004*b*). Our results support this conclusion and advance these earlier results by indicating that the effects of pollination are expressed through differences in phenology. In addition, the earlier study concluded, based on the pattern of spatial autocorrelation, that the mast dynamics of individual trees were likely to be related to some autocorrelated feature of the habitat (Liebhold et al. 2004*b*). Our results indicate that this feature is water availability as measured by xylem water potential.

Several studies have attempted to identify the drivers of spatial synchrony at large spatial scales comparable to the statewide analyses conducted here. Based on concordance between spatial synchrony in acorn production and key environmental factors along with significant spatial interspecific synchrony in acorn production by *Q. lobata* and the largely sympatric *Q. douglasii*, Koenig and Knops (2013) concluded that the Moran effect was the key driver of large-scale spatial synchrony in this species. Using the MRM analyses employed here allowing the simultaneous comparison of multiple factors, Haynes et al. (2013) concluded that weather—the Moran effect once again—was the primary driver of spatial synchrony in acorn production by oaks in the Northeastern United States and that proximity was not important after taking weather into account. Our results support these prior conclusions regarding the key role of the Moran effect in driving spatial synchrony of masting behavior.

More generally, the Moran effect has been identified as driving spatial synchrony in population dynamics of a variety of taxa from insect outbreaks (Peltonen et al. 2002, Haynes et al. 2013) to several mammalian species (Ranta et al. 1997, Post and Forchhammer 2002, Grøtan et al. 2005). As Haynes et al. (2013) pointed out, the MRM technique offers a powerful tool for disentangling the effects of environmental and non-environmental processes as potential drivers of population synchrony. Our results indicate that the relative importance of different spatial processes to the phenomenon of spatial synchrony is potentially dependent on the spatial scale being analyzed as well as the ecological system under consideration.

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