Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks

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Abstract. Seed production that varies greatly from year to year, known as "masting" or "mast-fruiting" behavior, is a population-level phenomenon known to exhibit geographic synchrony extending, at least in some cases, hundreds of kilometers. The two main nonexclusive hypotheses for the driver of such geographically extensive synchrony are (1) environmental factors (the Moran effect), and (2) the mutual dependence of trees on outcrossed pollen (pollen coupling). We tested 10 predictions relevant to these two hypotheses using 18 years of acorn production data on two species of California oaks. Data were obtained across the entire ranges of the two species at 12 sites (10 for each species) separated by up to 745 km. In general, our results provided strong support for the importance of the Moran effect as a driver of spatial synchrony in and between these two species. Particularly compelling was evidence of close concordance between spatial synchrony in acorn production and key environmental factors extending over the range of both species and significant spatial cross-synchrony between the two species, despite considerable differences in their geographical ecology. Because oaks are monoecious, female flowers are not necessarily related to pollen production, and thus, our tests do not address the role of pollen coupling in bisexual species where pollen and flower production are necessarily correlated. For the oak species considered here, however, the Moran effect is a key driver of large-scale spatial synchrony in acorn production.

Key words: acorn production; California, USA; mast-seeding; Moran's theorem; pollen coupling; Quercus douglasii; Quercus lobata; spatial synchrony.

INTRODUCTION

Highly variable but regionally synchronized seed production, known as mast-fruiting or masting behavior, is a conspicuous characteristic among many perennial plants and is particularly widespread among temperate trees (Silvertown 1980, Koenig and Knops 2000, Kelly and Sork 2002). Although their relative importance in most systems remains to be determined, the factors selecting for masting behavior potentially include both predator satiation and advantages associated with increased pollination success (Kelly and Sullivan 1997, Kelly and Sork 2002). Equally controversial are the factors that drive spatial synchrony (the coincident change in numbers by geographically disjunct populations), which, in some cases, including those involving seed production, can be on a geographic scale of hundreds of kilometers (Koenig and Knops 1998a, Post and Forchhammer 2002, Liebhold et al. 2004, Grøtan et al. 2005). Three factors have been identified as being potentially key to spatial synchrony in population dynamics: correlated environmental variables or the

"Moran effect" (Moran 1953, Royama 1992), dispersal of individuals or reproductive structures among populations, and trophic interactions with other species that are themselves synchronized due to one of the previous two factors (Liebhold et al. 2004).

Although seed predation has been implicated as being important in a few systems (Shibata et al. 1998, Lamontagne and Boutin 2007), the first two factors have generally been considered most likely to be driving spatial synchrony in seed production of forest trees. Supporting the importance of the Moran effect is considerable evidence that annual seed production is correlated with temperature and/or rainfall (Kelly and Sork 2002), which, given the typically large spatial scale of synchrony found in both temperature and rainfall globally (Koenig 2002), makes such environmental factors strong candidates for being important to spatial synchrony in annual seed production as well. On the other hand, the environmental factors correlating with annual seed production are, in the case of wind-pollinated temperate trees, often those likely to be affecting pollen availability or fertilization success (Koenig et al. 1996, Cecich and Sullivan 1999), and thus may be acting not just as cues for flowering and seed production (Kon and Noda 2007), but as factors directly influencing the availability or movement of

TABLE 1. Tests comparing the likely importance of pollen coupling vs. the Moran effect as factors driving spatial synchrony in acorn production of two species of California (USA) oaks.

Test and prediction	*Quercus lobata*	*Quercus douglasii*
1a) Key weather factors occur when pollen is being produced or dispersed (spring in year x)	yes (partly)	yes (partly)
1b) Key weather factors are those most likely to affect pollen availability	no	yes (partly)
2a, 4a) Spatial synchrony in key environmental variables $\geq$ spatial synchrony in acorn production	yes	yes
2b, 4b) "Spatial synchrony $\times$ distance" slopes similar for key environmental variables and acorn production	yes ($P = 0.34$)	yes ($P = 0.87$)
2c, 4c) Scale of spatial synchrony in acorn production	very large (>400 km)	very large (>400 km)
3a) Correlation between the pairwise correlations for acorn production and environmental variables	positive ($r = 0.44$, $P = 0.08$)	positive ($r = 0.35$, $P = 0.13$)
3b) Correlation between the within-year CVs for acorn production and the environmental variables	positive ($r = 0.73$, $P < 0.001$)	positive ($r = 0.71$, $P < 0.001$)

Note: Ellipses (...) indicate no prediction.

pollen. Given that outcrossing is the norm in many of these tree species (Hamrick and Godt 1989, Hamrick et al. 1992), this leads to the hypothesis that "pollen coupling" (the dependence of individuals on pollen produced synchronously by other individuals in these primarily outcrossing species) may drive spatial synchrony. In conjunction with resource storage, which is believed to be important based on temporal autocorrelation in seed production (Sork et al. 1993, Koenig et al. 1994b, Crone et al. 2009), theoretical studies confirm the potential for pollen coupling playing an important role in driving spatial synchrony within (Iwasa and Satake 2004) and even among (Tachiki et al. 2010) species, potentially generating synchrony among populations much farther apart than the distance of direct pollen exchange between trees.

These two hypotheses are not mutually exclusive, and it has proved difficult to distinguish between them, since both mechanisms may produce similar patterns of spatial synchrony (Liebhold et al. 2004). As a result, except in unusual cases when alternative factors can be eliminated (Grenfell et al. 1998, Rosenstock et al. 2011), most attempts to determine the relative importance of the two hypotheses have relied upon detecting correlations between observed spatial synchrony in the phenomenon of interest (in this case, seed production), and spatial synchrony in the weather factors potentially driving synchrony in seed production (Schauber et al. 2002, Post 2003).

Here, we go beyond such correlations in two ways using data collected on two species of California oaks differing in relative abundance and distribution in ways that might be expected to influence spatial synchrony if it is being driven by pollen coupling, but not if it is being driven by the Moran effect. First, we examined not only the relationship between spatial synchrony in environ-

mental factors known to correlate with seed production and spatial synchrony in seed production, but several additional relationships between seed production and environmental factors. Second, we examined spatial cross-synchrony between the two species, which, given that hybridization between them is rare, cannot be driven by pollen coupling.

HYPOTHESES AND PREDICTIONS

Weather variables correlating with seed production

To the extent that pollen coupling is an important driver of spatial synchrony in seed production, environmental events correlating with seed production should take place during either the period when pollen is being produced or pollen dispersal is taking place (test 1a). Although both rainfall and temperature could influence pollen production and availability in various ways, the potential effects of rain on pollen flow are direct and unequivocal, whereas those of temperature on pollen production or dispersal are less clear. Thus, we considered it more likely that rainfall would be the more important variable influencing acorn production if pollen coupling is important (test 1b). If the Moran effect is important, then environmental events affecting seed production may occur at any developmental time and may or may not be factors likely to affect pollen production or dispersal. These and the other predictions are summarized in Table 1.

Spatial scale of synchrony in seed production relative to key weather variables

Both pollen coupling and the Moran effect can potentially drive spatial synchrony in seed production. However, the Moran effect explicitly predicts that the "spatial synchrony $\times$ distance" relationship exhibited by

TABLE 1. Extended.

Q. lobata × Q. douglasii	Results consistent with:		Location of results
	Pollen coupling	Moran effect	
⋯	yes (partly)	⋯	Table 3
⋯	yes (partly)	⋯	Table 3
yes	⋯	yes	Fig. 2
yes (P = 0.97)	no	yes	Fig. 2
very large (>400 km); species not significantly different	no	yes	Fig. 2
⋯	no	yes	Fig. 3
⋯	no	yes	Fig. 3

the relevant environmental factors (that is, the regression of distance between sites on spatial synchrony between sites; the latter measured by the pairwise correlation coefficients) should be both at least as great as (test 2a), and similar in slope to (test 2b), the spatial synchrony × distance relationship observed in seed production. In contrast, pollen coupling predicts that the relationship between synchrony and distance in seed production is likely to be complex, being driven by geographic variation in wind, topography, and other factors affecting pollen availability. To the extent that this test relies on failing to reject the hypothesis of a difference between the slopes, there is a relatively high probability of a Type II error, and thus, it is not necessarily a strong test.

Theoretically, pollen coupling can drive spatial synchrony on a scale larger than the distance of direct interaction (i.e., cross-fertilization) between trees (Satake and Iwasa 2002a). It is unclear exactly how much farther, however. There is the further complication that the distance of direct interaction among trees is also unclear. Recent work on Quercus lobata at one of our sites (Sedgwick Reserve), for example, has indicated short mean weighted pollination distances of only 114 m using indirect methods (Pluess et al. 2009), whereas work at a second site using direct paternity assignment (Hastings Reservation) found that the majority of effective pollen travels >200 m (Abraham et al. 2011), a result that appears to be more typical for wind-pollinated forest trees (Ashley 2010). In any case, it appears unlikely that direct interaction is common among trees greater than a few kilometers apart, or that spatial synchrony on a scale of >100 km could be driven primarily by pollen coupling. Thus, the existence of synchrony at such large spatial scales would confirm

the importance of the Moran effect, although it would not reject a role for pollen coupling (test 2c).

Relationship between weather and seed production across sites and among years

If environmental factors are driving spatial synchrony in seed production, then across all pairs of sites, the correlations between acorn production should themselves be correlated with the pairwise correlations in the relevant environmental factors between the sites (test 3a). Furthermore, there should be a positive correlation across years between the relative variability in seed production and the relative variability in the relevant environmental factors (test 3b). Neither of these relationships are predicted by pollen coupling. These tests address similar statistical relationships examined by tests 2a and 2b, although in a form sufficiently different to warrant consideration.

Spatial cross-synchrony between species

Spatial synchrony between species (spatial cross-synchrony) cannot be driven by pollen coupling in these wind-pollinated species between which hybridization is rare (Craft et al. 2002, Abraham et al. 2011). Thus, spatial cross-synchrony, particularly at large geographic scales, is only likely to be significant if the Moran effect is a key driving force (test 4c). Indeed, given the considerable spatial synchrony exhibited by both rainfall and temperature (Koenig 2002), and the fact that the two species have generally overlapping geographic ranges, the Moran effect would be consistent with the relationship between spatial synchrony in acorn production and distance being similar for the two species, despite differences in relative abundance across their ranges.
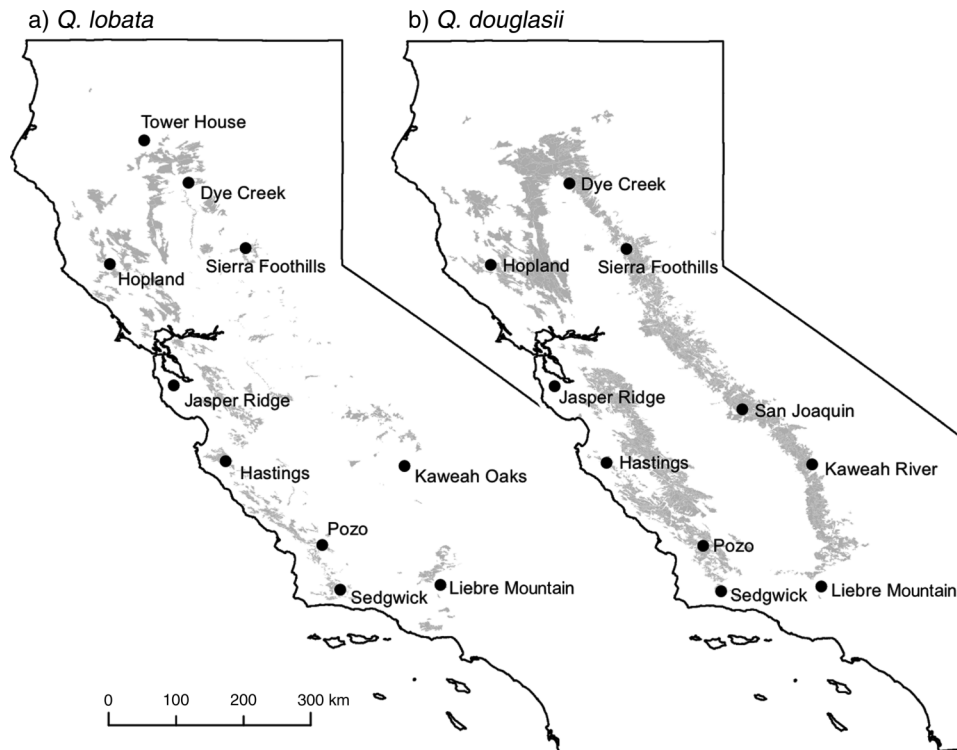
FIG. 1. The distribution of the two oak species, (a) *Quercus lobata* and (b) *Quercus douglasii*, in California, USA, and the sampling sites used in the analyses.

In contrast, these results are unlikely if pollen coupling is the main driver of spatial synchrony. Specifically, assuming similar phenology patterns, pollen coupling predicts that spatial synchrony is likely to be much greater in a species where individuals (and thus presumably pollen) are common and more evenly distributed, as is the case for *Quercus douglasii*, than in a species in which individuals are relatively uncommon and unevenly distributed such as *Q. lobata* (Fig. 1).

As with spatial synchrony within species, spatial cross-synchrony in the key environmental variables between the two species should be as great or greater than cross-synchrony in acorn production between the species (test 4a), and the "spatial cross-synchrony × distance" slope for the environmental variables should be statistically indistinguishable from that for acorn production between the species (test 4b). As with test 2b, the probability of a Type II error for this test is high.

Some degree of spatial cross-synchrony between these two species could be driven by pollen coupling to the extent that similar patterns of pollen availability are independently driving similar patterns of spatial synchrony in the two species, or to the extent that species are competing for limited pollinators (Tachiki et al. 2010). In the case of wind-pollinated species with very different abundance patterns, however, no significant spatial cross-synchrony is likely beyond distances of a

few kilometers if pollen coupling is a primary driving force behind such synchrony.

MATERIALS AND METHODS

Study sites and species

To test these predictions, we gathered data on the annual seed production on 506 individually tagged trees of two species of California (USA) oaks over a period of 18 years (1994–2011) at 12 sites throughout the state (Table 2). Species considered were the valley oak *Quercus lobata* (10 sites, 250 trees) and blue oak *Q. douglasii* (10 sites, 256 trees).

These species were chosen for several reasons. Both species are "white oaks" in the subgenus *Lepidobalanus*, mature acorns in a single season, are California endemics, and are often sympatric across their ranges, which include foothill regions ringing the Central Valley of California up to ~1800 m elevation (Griffin and Critchfield 1972). Both species are winter deciduous and exhibit similar phenology, flowering in early spring and maturing acorns several months later in the autumn. The total estimated area over which the species are found within the state are very different, however, being an estimated 13 751 km^2 for *Q. douglasii* and only 1967 km^2 for *Q. lobata*, a sevenfold difference (Bolsinger 1988). Within these ranges, mean estimated stand volume of the species are 223 m^2/ha for *Q. lobata* and

TABLE 2. Sampling localities for the two species of oaks considered in this study in California, USA.

Site	County	Latitude (north)	Longitude (south)	Number of trees (N)	
				Q. lobata	*Q. douglasii*
Tower House Historic District	Shasta	40°38′	122°34′	17	0
Dye Creek Preserve	Tehama	40°08′	122°00′	18	22
Sierra Foothills Research and Extension Center	Yuba	39°15′	121°25′	9†	25
Hopland Research and Extension Center	Mendocino	38°58′	123°07′	10‡	20
Jasper Ridge Biological Station	San Mateo	37°24′	122°13′	39	29
San Joaquin Experimental Range	Madera	37°07′	119°45′	0	25
Kaweah River	Tulare	36°21′	118°47′	0	14‡
Kaweah Oaks Preserve	Tulare	36°19′	119°10′	10‡	0
Hastings Natural History Reservation	Monterey	36°12′	121°33′	86	56
Pozo	San Luis Obispo	35°16′	120°16′	24	25
Liebre Mountain	Los Angeles	34°44′	118°41′	11	20
Sedgwick Reserve	Santa Barbara	34°43′	120°02′	12; 26§	20

Note: All localities were sampled each year between 1994 and 2011, except where noted.
† Added in 2001.
‡ Added in 1999.
§ Twelve trees were surveyed 1994–2007; 14 additional trees were added in 2008.

only 87 m^2/ha for *Q. douglasii*; differences that are due to stands of *Q. lobata* generally containing few large trees, while those of *Q. douglasii* typically contain many small trees (White 1966, Bolsinger 1988).

The relative abundance of 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 see in 15 s (Koenig et al. 1994*a*, *b*). Values analyzed were the geometric mean of all individuals of a species counted at a site. Specifically, counts by the two observers were added (N30; count over 30 s), log-transformed (ln[N30 + 1] = LN30) to reduce the correlation between the mean and the variance, and then averaged across all individuals at a site to estimate mean acorn production for that year and at that particular site for each species; site means are provided in the Supplement. In order to confirm that site means adequately reflect the overall patterns of spatial synchrony, we compared spatial synchrony using site means with that using individual trees.

Analysis of weather variables

We used records of monthly rainfall, mean maximum, and mean minimum temperatures, matched geographically to the 12 sites, obtained from the PRISM climate group (Oregon State University, Corvallis, Oregon, USA; data *available online*).[5] PRISM values are estimated by means of parameter-elevation regressions based on data from available weather stations; a comparison of the PRISM data between 1980 and 2010 for annual rainfall and mean maximum April temperatures at Hastings Reservation, for which daily records were available, confirmed high correlations between the two measures (annual rainfall, $r = 0.97$, t_{29}

[5] http://prism.oregonstate.edu

$= 20.4$; mean maximum April temperature, $r = 0.89$, $t_{29} = 10.7$; both $P < 0.0001$).

To determine the environmental variables correlating with acorn production, we first standardized all weather variables to mean = 0 and standard deviation = 1 in order to ensure that their scales were comparable (Schielzeth 2010). We then performed mixed-effects models for both species in which mean LN30 was the dependent variable and "site" was included as a random factor. All analyses were conducted in R 2.10.1 (R Development Core Team 2010).

Environmental factors included as independent variables encompassed all potentially vulnerable periods in acorn development. For both species, acorns come from buds initiated in spring of year $x - 1$ that flower and are fertilized in the spring of year x (Sork et al. 1993, Koenig et al. 1996, Cecich and Sullivan 1999). Thus, we included the following 14 weather variables, listed in reverse chronological order: (1) mean maximum summer temperature (May through August [year x]); (2) mean maximum April temperature (year x); (3) rainfall in April (year x); (4) mean maximum March temperature (year x); (5) rainfall in March (year x); (6) mean minimum winter temperature (November [year $x - 1$] through February [year x]); (7) winter rainfall (November [year $x - 1$] through February [year x]); (8) the prior year's mean maximum autumn temperature (September through November [year $x - 1$]); (9) the prior year's mean maximum summer temperature (May through August [year $x - 1$]); (10) the prior year's mean maximum April temperature (year $x - 1$); (11) the prior year's rainfall in April (year $x - 1$); (12) the prior year's mean maximum March temperature (year $x - 1$); (13) the prior year's rainfall in March (year $x - 1$); and (14) the prior year's winter rainfall (November [year $x - 2$] through February [year $x - 1$]). Note that the study sites experience a mediterranean climate in which the vast majority of precipitation falls during the winter, while

summers and early autumn (June–September) are uniformly dry.

Using the parameter estimates of variables significant ($P < 0.05$) in the complete model, we then multiplied the effect size of each significant environmental variable by the (standardized) value for each site to derive a single synthetic environmental variable (henceforth "combined EV") that best encapsulated the environmental factors affecting annual acorn production in that species across all sites sampled. This combined EV variable was used in all subsequent tests of environmental forcing of spatial synchrony in acorn production.

We performed two additional tests of the relationship between the combined EV and acorn production. First, for each pair of sites, we calculated the Pearson correlation between the annual combined EV values, and the correlation between the mean annual LN30 values. We then plotted the two sets of r values against each other and tested them using 1000 bootstrap trials in which significance was determined from the mean ± standard error (SE) of the correlation coefficient derived from the bootstrap trials (test 3a). This test addresses the same relationship examined by test 2b, but using a different approach. Second, for each year, we calculated the coefficient of variation (CV = [standard deviation × 100]/mean) in the combined EV values vs. the CV of acorn production, in both cases calculated across all sites (test 3b).

Spatial synchrony and spatial cross-synchrony

Spatial synchrony between populations of the same species (tests 2a, 2b, and 2c) and spatial cross-synchrony between populations of different species (tests 4a, 4b, and 4c) was estimated using the modified correlogram technique (Koenig and Knops 1998b), binning sites into three distance categories (0–200 km, 200–400 km, and >400 km; the maximum distance between sites was 745 km (Q. lobata) and 667 km (Q. douglasii) (Fig. 1). Statistical testing of synchrony was performed by bootstrapping in which n pairwise correlations out of those within the given distance category were chosen randomly with replacement for each trial, where n = the number of sites involved in the complete set of pairwise correlations within the given distance category. In each case, we performed 1000 trials and significance was estimated by calculating a z value from the mean and SE, the latter calculated as the standard deviation of the trial means (Efron and Tibshirani 1986, Bjørnstad et al. 1999). Analyses were performed separately for acorn production using the mean annual LN30 values for all individuals sampled at each site and for the combined EV values for that population. Since spatial synchrony cannot, on average, be significantly negative, we used one-tailed z values for statistical significance when testing for spatial synchrony. This is not true for spatial cross-synchrony, for which we used two-tailed z values.

In general, spatial synchrony, when it exists, is expected to decline with distance (Koenig 1999, Liebhold et al. 2004). In order to test differences between the species and the combined EV values for the "spatial [cross-]synchrony × distance" relationship (i.e., the slope of the regression of distance on synchrony; test 2b), we performed sets of 1000 bootstrap trials, choosing n pairwise correlations randomly with replacement from each set of pairwise correlations being compared, where n = the number of different sites in the analysis. For each trial, we then performed an ANCOVA in which the correlation coefficients were the dependent variable and the independent variables were distance between sites, the "type" involved (i.e., whether values were for acorn production or combined EV values), and the interaction between the two. We then calculated the mean ± SE (estimated by the standard deviation of the mean effect size) for the interaction over all trials and estimated statistical significance by the two-tailed z value (Efron and Tibshirani 1986).

Finally, we compared the magnitude and the slopes of the spatial synchrony × distance relationship for the two species using a likelihood ratio test (test 4b). Specifically, we bootstrapped 1000 sets of pairwise correlations from each of the species, choosing n_i pairwise correlations for each species, where n_i = the number of sites with data for species i. We then determined the effect size associated with the species term and the deviance associated with an ANCOVA excluding the distance × species interaction compared to the model including the interaction term (Dalgaard 2008). Statistical significance for the difference in magnitude of spatial synchrony was estimated by the z value associated with the mean ± SE of the species term, while significance of the difference in slopes was estimated from the χ^2 value associated with mean of the deviances from the trials excluding the distance × species interaction term.

RESULTS

Analysis of environmental variables

Four variables were significant in the mixed-effects model of Q. lobata acorn production, including mean maximum April temperature, mean maximum April temperature lagged one year, mean maximum March temperate lagged one year, and winter rainfall lagged one year (test 1a; Table 3). For Q. douglasii, seven variables were significant, including mean maximum March and mean maximum April temperatures, March rainfall, winter rainfall, mean maximum autumn temperature, rainfall in April lagged one year, and winter rainfall lagged one year. Thus, temperatures during the primary period of pollen production and dispersal were significant in both species, while rainfall in March was significant only for Q. douglasii (test 1b).

Spatial synchrony

Mean spatial synchrony of the two species was significant across all distance categories using both site

TABLE 3. Effect sizes (mean ± SE) for the environmental variables significant in the mixed-effects models of annual mean acorn production for the two oak species in reverse chronological order.

Year and variable	Q. lobata	Q. douglasii
0		
Mean maximum summer temperature	ns	ns
Mean maximum April temperature	0.579 ± 0.158***	0.438 ± 0.141**
Rainfall in April	ns	ns
Mean maximum March temperature	ns	−0.341 ± 0.114**
Rainfall in March	ns	−0.233 ± 0.081**
Mean minimum winter temperature	ns	ns
Winter rainfall	ns	−0.171 ± 0.081*
Mean maximum autumn temperature	ns	0.313 ± 0.109**
−1		
Mean maximum summer temperature	ns	ns
Mean maximum April temperature	−0.312 ± 0.137*	ns
Rainfall in April	ns	0.319 ± 0.096**
Mean maximum March temperature	−0.277 ± 0.124*	ns
Rainfall in March	ns	ns
Winter rainfall	0.282 ± 0.116*	0.333 ± 0.082***
Sites (years of data)	10 (177)	10 (184)

Note: Italicized variables are those likely to be during the primary period of pollen production and dispersal.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

means and individual trees (test 2a; Fig. 2a, b). Although the absolute degree of synchrony is (unsurprisingly) greater using site means than individual trees, there was no significant difference between the synchrony × distance slopes using site means vs. individual trees for either species (Q. lobata, mean $\chi_1^2 = 0.6$, $P = 0.5$; Q. douglasii, mean $\chi_1^2 = 0.1$, $P = 0.9$), and thus, we used site means in all subsequent analyses.

The two species did not differ in either their absolute magnitude of synchrony (mean z value = 0.2, $P = 0.6$; test 4c) or their synchrony × distance slopes (mean $\chi_1^2 = 1.8$, $P = 0.19$; test 4b). There was also no significant difference between the synchrony × distance and the combined EV × distance slopes for either species (both $P \geq 0.35$; test 2b; Fig. 2d, e). Pairwise correlation coefficients for the combined EVs vs. those for acorn production (test 3a; Fig. 3a, b) and for the CVs in the combined EVs across sites within years vs. the CVs in acorn production across sites within years (test 3b; Fig. 3c, d) were all positive ($0.35 < r < 0.73$), and significant or nearly so ($P \leq 0.13$; Fig. 3a, b).

Spatial cross-synchrony

There was highly significant spatial cross-synchrony between Q. lobata and Q. douglasii using both individual trees and site means (test 4a; Fig. 2c). As with the individual species, there was no significant difference in the slopes of the regression of distance on spatial cross-synchrony using individuals compared to site means ($\chi_1^2 = 0.1$, $P = 0.9$), and thus, site means were used in subsequent analyses. There was no significant difference in the slopes of the regression of distance on spatial cross-synchrony in acorn production compared to the regression of distance on spatial cross-synchrony in the

combined EVs of the two species (mean $\chi_1^2 = 1.1$, $P = 0.28$; test 4b; Fig. 2f).

DISCUSSION

There is significant spatial synchrony in annual acorn production in both Q. lobata and Q. douglasii extending across sites up to nearly 750 km apart. For both species, this means that, in a good year, a large pulse of resources (Ostfeld and Keesing 2000) is made available to wildlife over large geographic areas by virtue of the synchronous acorn production by millions, or (in the case of Q. douglasii) tens of millions, of trees. Although previous studies have found spatial synchrony of both seed production and population size extending over large areas (Koenig and Knops 1998a, Post and Forchhammer 2002, Liebhold et al. 2004, Grøtan et al. 2005), this may be the first documentation of such high synchrony extending over the entire range of such geographically widespread species.

What drives this striking degree of synchrony? One possibility is the Moran effect, which hypothesizes that synchrony in acorn production is being driven by synchrony in environmental factors used by trees as cues to determine reproductive investment. Since environmental factors such as temperature and rainfall are themselves spatially synchronous (Koenig 2002), the Moran effect can potentially drive spatial synchrony over large geographic areas. Alternatively, the dependence of trees on pollen from neighboring individuals, in conjunction with resource storage, has been shown theoretically to potentially generate spatial synchrony in seed production between trees located far beyond the distance that trees directly interact via pollen exchange (Satake and Iwasa 2002a, b). Distinguishing between these hypotheses is difficult, since they are not mutually
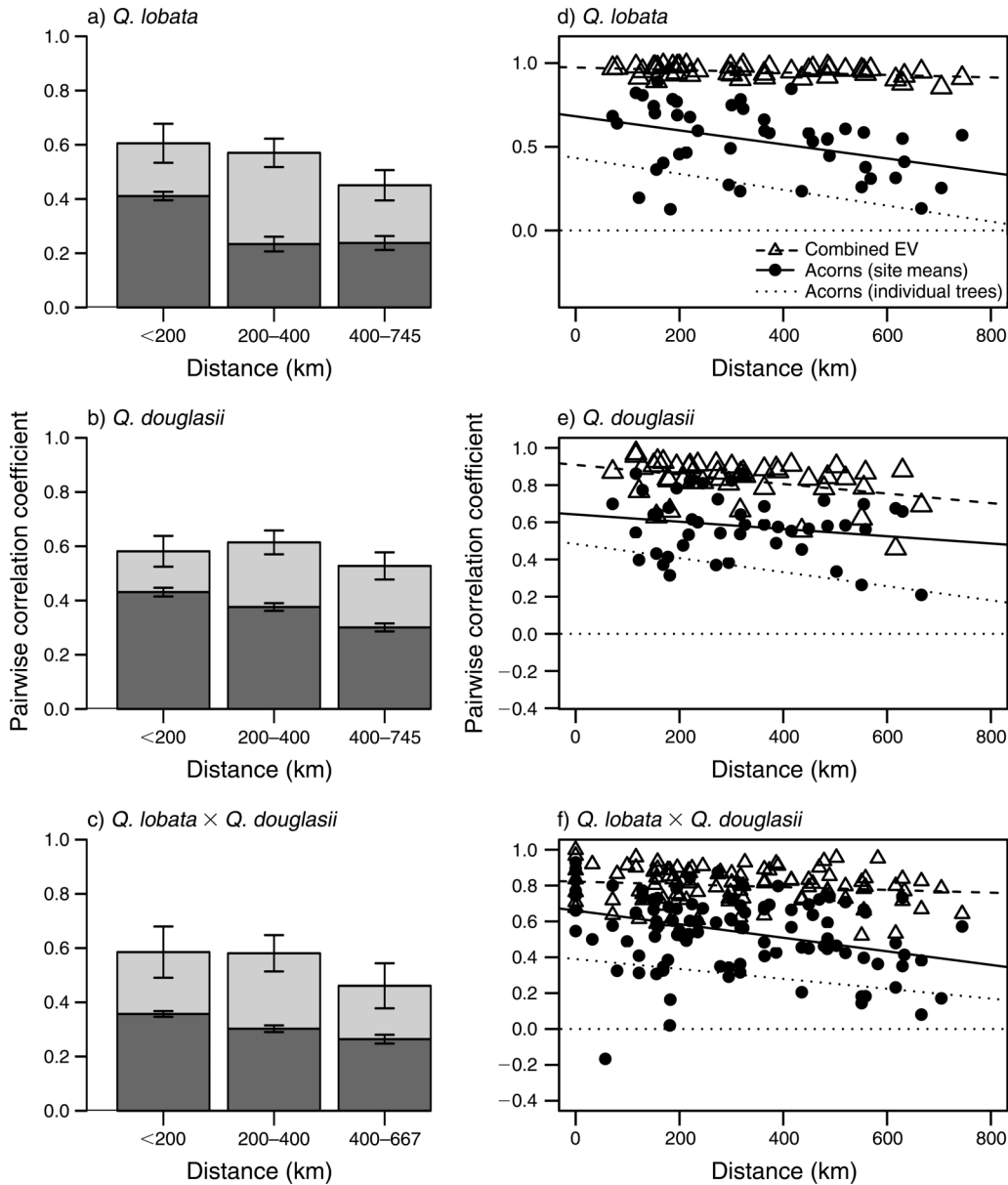
FIG. 2. (a–c) Spatial synchrony histograms (pairwise correlation vs. distance; mean with 95% confidence interval) for *Quercus lobata*, *Quercus douglasii*, and *Q. lobata* × *Q. douglasii* (i.e., spatial cross-synchrony between the two species); values in light gray fill are based on site means; values in dark gray fill are based on analyses using individual trees. Confidence intervals are based on randomization tests dividing data into three distance categories (0–200 km, 200–400 km, 400–[maximum distance between sites], in km); all are significantly >0. (d–f) Scattergrams of spatial synchrony (pairwise correlation coefficients) for the combined environmental variable ("combined EVs" [see *Materials and methods: Analysis of weather variables*]; open triangles and dashed line) and acorn production (solid circles and solid line show site means, and the dotted line shows individual trees) for *Q. lobata*, *Q. douglasii*, and *Q. lobata* × *Q. douglasii*.

exclusive and are capable of generating similar patterns of spatial synchrony (Liebhold et al. 2004).

Here we tested these hypotheses by means of a series of 10 predictions regarding the patterns exhibited by, and the relationships between, spatial synchrony in acorn production and the environmental factors correlating with acorn production (Table 1). In general, the Moran effect predicts a close relationship between the

two whether dealing with synchrony within species or cross-synchrony between species. Furthermore, the Moran effect predicts that spatial synchrony in key environmental factors should be as high, or higher than, that in acorn production, and that the spatial synchrony × distance relationships in acorn production, and the key environmental factors should exhibit similar slopes. Two other predictions of the Moran effect include (1) a
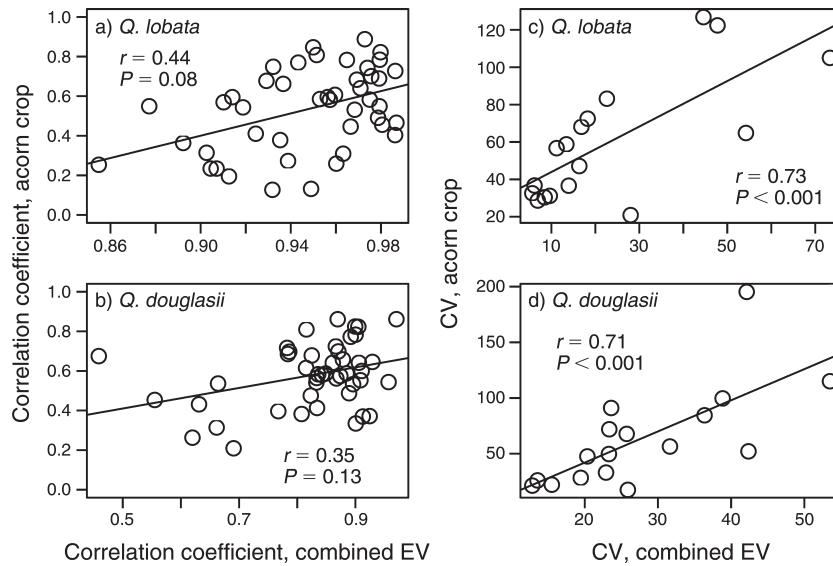
Fig. 3. (a, b) Scatterplots of the pairwise correlation coefficients between sites for the combined environmental variables (combined EVs) on the x-axis vs. the mean acorn crop (y-axis) for Q. lobata and Q. douglasii. (c, d) Scatterplots of the coefficients of variation (CV) across sites for each year calculated using the combined EVs (x-axis) vs. CVs across sites for each year calculated from the mean acorn crop values (y-axis) for Q. lobata and Q. douglasii. Individual correlation coefficients (r values) and P values are listed for each panel.

positive correlation between the pairwise correlations between acorn production and the pairwise correlations between environmental variables across sites, and (2) a positive correlation between the within-year CVs for acorn production and the within-year CVs of the environmental variables across years. In other words, if environmental factors are driving spatial synchrony in acorn production, there should be a positive relationship between both synchrony in acorn production and synchrony in environmental factors across sites and between the relative variability in acorn production and the relative variability in the relevant environmental variables across years.

As found in previous studies (Sharp and Sprague 1967, Sork et al. 1993, Koenig et al. 1994b), acorn production in the two species, both of which are in the "white oak" subgenus, were both strongly related to weather conditions during the spring flowering period. Thus, as predicted by pollen coupling (García-Mozo et al. 2007), at least some of the key weather factors correlating with acorn production in these species take place when pollen is being produced and dispersed. Rainfall in the spring, a variable particularly likely to influence pollen flow, was only significant for Q. douglasii, however. The environmental variable most important to acorn production in these species (temperature) also encompassed the period of pollen production and flow (test 1a), but is less likely to directly affect pollen dispersal (test 1b). Thus, these results are ambiguous but provide some support for the importance of pollen coupling.

All of the remaining tests yielded results consistent with the Moran effect being an important driver of spatial synchrony in acorn production by these species, at least at the relatively large spatial scale that was the focus of our analyses. Although pollen coupling does not specifically predict an alternative pattern in some cases, our results are unlikely in the absence of a strong Moran effect. In particular, there is no a priori reason to expect the spatial synchrony × distance slopes to be similar for the different species unless synchrony in acorn production is being driven by similar factors (that is, the environment) despite the differences in geographical ecology of the two species. Spatial synchrony is also expected to be large, encompassing much or all of the geographic range of these species, only if it is being driven by environmental factors. This is unambiguously true for spatial cross-synchrony, since pollen coupling cannot be driving significant synchrony in acorn production over large distances between these species given that they are wind pollinated and do not hybridize frequently.

Our results thus provide strong support for the importance of the Moran effect as the main synchronizer of acorn production both within and between these two species, at least at the large geographic distances analyzed here that are beyond the range of any plausible influence of pollen coupling. In general, we did not find strong support for pollen coupling as a driver of spatial synchrony, although our analyses do not reject the likelihood that it plays a role, at least at relatively short distances. There is an additional problem in terms of defining what, exactly, "pollen coupling" entails. Satake and Iwasa (2002a, b) use it to refer to the situation, typical in many angiosperms, of species with bisexual or hermaphroditic flowers in which the production of

female flowers and pollen production are related. In contrast, oaks are monoecious, and thus, female flowers and pollen production are at least potentially independent, and it is possible that pollen availability is itself being driven by environmental factors. To the extent that this is true, we are not testing pollen coupling sensu Satake and Iwasa (2002*a, b*), but rather Moran effects at different levels (E. Crone, *personal communication*). It is thus unsurprising that our tests fail to provide strong evidence that pollen coupling drives spatial synchrony in these species. Rather, the strength of our findings is primarily in their strong support for a key role for the Moran effect.

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SUPPLEMENTAL MATERIAL

Supplement

Site means (mean number of acorns counted per 30 seconds) and environmental data (from the PRISM database) used in the analyses (1994–2011) (*Ecological Archives* E094-009-S1).