Phenological synchrony does not regulate fecundity in a mast-fruiting oak species

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Abstract

Biologists have long debated why some plant species produce many seeds synchronously during some years and few during others. One hypothesis is that selection on phenological synchrony of flowering improves pollination efficiency and leads to increased fecundity. In an 11-year study of valley oak (*Quercus lobata*), we found that, indeed, trees that produced flowers during mid-season tended to produce more acorns. But, is synchrony the key factor? Here, we test the phenological synchrony hypothesis versus the alternative hypothesis that the environment principally shapes flowering phenology and acorn production. At our site, we find that a tree's microenvironment is associated with both timing of phenology and acorn production. Timing of flowering depends on air temperature and crop size is not related to synchrony but is best predicted by relative elevation – likely a proxy for substrate quality and access to water. We conclude that microenvironment - not phenological synchrony - shapes acorn production.

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Abstract

Biologists have long debated why some plant species produce many seeds synchronously during some years and few during others. One hypothesis is that selection on phenological synchrony of flowering improves pollination efficiency and leads to increased fecundity. In an 11-year study of valley oak (*Quercus lobata*), we found that, indeed, trees that produced flowers during mid-season tended to produce more acorns. But, is synchrony the key factor? Here, we test the phenological synchrony hypothesis versus the alternative hypothesis that the environment principally shapes flowering phenology and acorn production. At our site, we find that a tree's microenvironment is associated with both timing of phenology and acorn production. Timing of flowering depends on air temperature and crop size is not related to synchrony but is best predicted by relative elevation – likely a proxy for substrate quality and access to water. We conclude that microenvironment - not phenological synchrony - shapes acorn production.

Introduction

Synchronous fluctuations in inter-annual seed production, known as masting, is common in woody plant species, especially long-lived trees (Janzen 1978; Silvertown 1980; Sork 1993; Kelly 1994); Kelly and Sork (2002). The study of masting has a long history (Koenig 2021), not only because the intermittent production of seeds can be quite dramatic in some species but because this inter-annual variation in seed crop has cascading effects on associated food webs and ecosystem processes. Catalyzed by the classic papers of Janzen (1971; 1974) and Silvertown (1980), approximately 7500 studies of masting have been published in the past half-century debating various explanations for the phenomenon (Koenig 2021). One widely cited explanation is the predator satiation hypothesis (Zwolak *et al.* 2022), which says that the intermittent production of large seed crops satiates the seed predators so that some seeds survive during mast years (Janzen 1971; Janzen 1974; Kelly 1994; Kelly & Sork 2002). However, another non-mutually exclusive explanation has been proposed to promote the evolution of masting, which is the phenological synchrony hypothesis. It states that increased pollination efficiency resulting from more synchronous production of flowers leads to larger seed crops (Nilsson & Wastljung 1987; Smith *et al.* 1990; Kelly & Sullivan 1997; Tisch & Kelly 1998; Kelly & Sork 2002; Koenig *et al.* 2012; Koenig *et al.* 2015). In a given year, whether a tree flowers relatively earlier, later, or is in synchrony with the majority of other flowering trees can determine pollination success and seed production. If individual variation in seed production is due to genetic differences among trees, then selection would favor those traits that result in "good" and "bad" seed producers. For example, some evidence suggest that early and late flowering trees have lower acorn production than those that flower more synchronously with the rest of the population (e.g., Satake 2004; Koenig *et al.* 2015; Bogdziewicz *et al.* 2017; Bogdziewicz *et al.* 2020b). In an elegant test of this hypothesis, Bogdziewicz *et al.* (2020b) used an experimental approach to demonstrate pollen limitation in asynchronous trees in *Quercus ilex*. However, selection can only act against those asynchronous trees within a population if early or late flowering results in reduced reproductive success **and** their asynchrony has a genetic basis. If asynchrony is due to the environment, then selection will have not evolutionary response.

The goal of this study is to quantify the extent to which the microenvironment of individual trees accounts for individual variation in timing of flowering and variation in fecundity among valley oak (*Quercus lobata* Née) adults in a population in central coastal California. For many deciduous tree species, the timing of budburst, leaf expansion, and flower emergence is influenced by winter and spring temperatures and precipitation, which in turn can shape the length of the growing season, the risk of early spring frost damage, and the effectiveness of pollination (Sharp & Chisman 1961; Sharp & Sprague 1967). Valley oak is an ideal species to examine this question because its pattern of seed production fits that of a masting species in that it synchronously produces large crops every 4-5 years across populations(Koenig *et al.* 1996) and within our study population (VL Sork and A Lentz, unpublished data). Moreover, valley oak is a species of conservation concern. It has lost much of its distribution since the arrival of the Europeans due to habitat transformation that has destroyed and fragmented many populations, and seedling recruitment is limited within the remnant populations (Tyler *et al.*

2006). Thus, understanding the role of the local biophysical environment on flowering and fruiting will give insight about the vulnerability of this foundation species to climate change (Ascoli *et al.* 2021).

To assess the relationship between tree site quality, flowering, and fecundity, we investigate the response of individual trees to micro-environmental variation across an 11-year period. We test the hypothesis that phenological synchrony of flowering is a major driver of masting (Koenig *et al.* 2012; Koenig *et al.* 2015; Bogdziewicz *et al.* 2020b). Specifically, this hypothesis predicts selection should disfavor trees that flower early and late in the season due to pollen limitation and favor trees that flower synchronously during mid-season through their improved reproductive success. To test whether phenological synchrony plays a role in masting, we ask several questions. **First**, is there evidence that the timing of flowering or synchrony of flowering correlates with acorn production? **Second**, is timing of flowering or synchronicity environmentally determined? That is, are the timings of emergence of staminate flowers (male inflorescences or catkins) and pistillate (female) flowers across trees within a population correlated with climate variables associated with their geographic location? In this study, we discover the same pattern of reduced acorn production for early and late flowering trees as Koenig *et al.* (2012), who presents these trends as evidence of stabilizing selection favoring population synchrony. But here, we document that microenvironmental variation is associated with significant intra-population variation in flower phenology and fecundity. We find little evidence for selection on floral timing or synchrony, which would provide support for the pollination efficiency hypothesis linking masting to phenological synchrony.

Methods and Materials

Study species and study site

Quercus lobata Née (California valley oak) is a signature tree of California oak savanna and woodland habitats. The species prefers deep loamy soils - principally below 600 m above sea level (asl) in the Central Valley, surrounding valleys, and foothills (Pavlik *et al.* 1991). Like all oaks, *Q. lobata* is a diploid, wind-pollinated, monoecious, and predominantly outcrossing tree species (Sork *et al.* 2002). Trees flower from February through April before and during leaf emergence, with the male inflorescences (catkins) emerging before the pistillate (female) flowers. If successfully fertilized, the latter develop into acorns over the summer and drop between September and November of the same year.

The study site is located in the Sedgwick Reserve, which is administered by the University of California at Santa Barbara as part of the University of California Natural Reserve System. The 2,380-ha reserve is 10 km northeast of Santa Ynez (Santa Barbara County, CA, USA) in the foothills of the San Rafael Mountains. The study trees are located in the Figueroa Creek valley (34°42 N, 20°02 W) at elevations ranging from 270 to 365 m asl. Tree density in this area averages ~1.5 trees/ha, tree breast height diameters average 101 cm (range 42 - 172 cm), and crown areas average 318 m^2 (range 65 – 655 m^2).

Despite the narrow elevational range of study trees, several important environmental factors co-vary with elevation, notably geology, soils, and thermal microclimates related to cold air pooling (**Figure 1**). The valley floor is underlain by recent Quaternary alluvial fill that can exceed

10 m in thickness and is composed of interlayered gravels, sands, silts and clay lenses. Overlying soils are deep, well-drained silty clay loams of the Salinas and Elder soil series (Shipman 1972). At slightly higher elevations, <5 m thick Quaternary pediment deposits from side canyons overlay this fill in some areas. Side slopes above ~330 m are underlain by older, weakly consolidated alluvial conglomerate or gravel of the Quaternary Paso Robles Formation (Dibblee 1950). Hillslope soils are mainly mapped as Shedd silty clay loam and Chamise shaly loam (Shipman 1981).

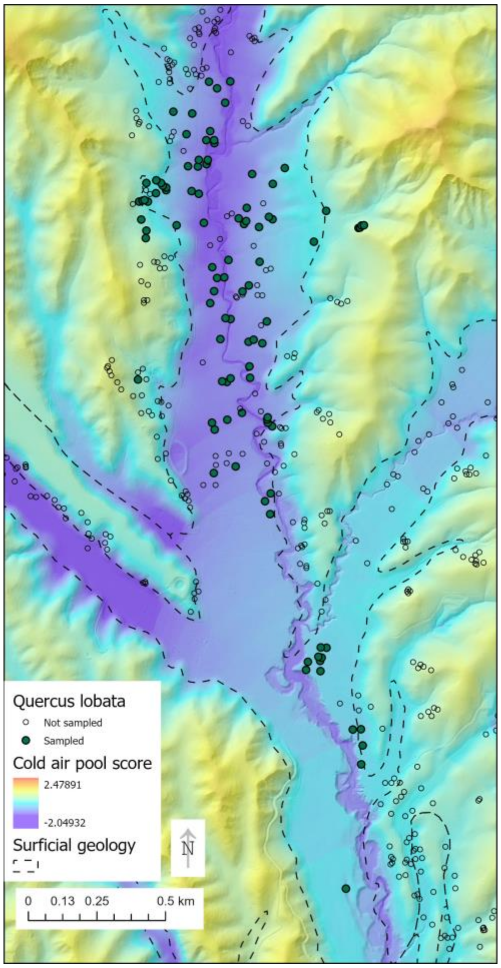

Figure 1. Map of study area showing the location of valley oaks (filled green circles are monitored trees, open circles are other valley oak adults in the study area) on a shaded relief image with cold air pooling index superimposed. The dashed line shows the approximate boundary between recent Quaternary alluvial fill and the Quaternary Paso Robles conglomerate. The active, meandering Figueroa Creek channel runs north-south down the valley. Study area is within the UC Santa Barbara Sedgwick Reserve, Santa Ynez Valley, Santa Barbara Co., CA, USA.

Cold air draining from the San Rafael Mountains frequently pools in the Figueroa Creek valley so that mean minimum daily temperatures during the flowering season are 1-3 °C lower on the valley floor than at elevations 25-75m higher on adjacent hillslopes. This difference produces visually striking elevational gradients in the timing of valley oak flower phenology across this landscape, with trees at higher elevations flowering earlier than individuals on the valley floor.

Data Collection

In 2007, we selected 100 valley oak adults across the valley floor and along the slopes of Figueroa Creek valley at our study site (**Figure 1**), but 3 trees died over the course of the study. For this study, we are using 97 trees surveyed from 2008 through 2019. From February through mid-April, we inspected trees for the emergence of flowers and leaves twice per week once their buds emerged until the leaves were fully developed. We classified the development of staminate flowers (male catkins with pollen), leaves, and pistillate flowers (female), which emerged in that order, into stages based on the prior studies of flower phenology in white oaks, section *Quercus* (Sharp & Chisman 1961; Sharp & Sprague 1967; Sork *et al.* 1993) as summarized in **Table 1**.

In the Fall of each year, we estimated acorn crop size by counting the number of acorns seen through binoculars in a 15 second interval twice (either two observers or one observer twice) using the Koenig visual survey method (Koenig *et al.* 1994a).

Table 1. Classification of developmental states of flowers and leaves in oaks.

	Staminate flowers	**Leaves**	**Pistillate flowers**
State 1	Catkin buds emerged	Leaf buds emerged	Flower buds appear
Stage 2	Catkins elongated and pollen released	Leaves apparent with petioles	Flowers visible within leaf petiole at leaf state 2
Stage 3	Catkins dry and/or dehisced	Leaves full-sized	Stigma brown and non-receptive

Beginning January 1, 2010, the thermal regime of a subset of 50 trees was monitored using Thermochron iButtons© that were mounted on the north side of trees at ~1.4m above the ground surface. Temperature was recorded every four hours.

Data Analysis

We derived daily minimum, maximum, and mean daily temperatures for each monitored tree and then averaged those values for January 1 – April 30 to estimate flowering season minimum, maximum and mean daily temperatures for each tree and for the population as a whole.

Thermal microclimate for all 97 trees was modeled using a 3m digital elevation model of the study area that was produced from 1m LIDAR data acquired by the National Center for Airborne Laser Mapping in November, 2020. We compared several indices of cold air pooling (Davis *et al.*

2019) – all highly correlated – and for the analyses here use the index introduced by Ashcroft and Gollan (2013):

$$CAP = \log(z - \min(z(d))) \quad \text{(Eq. 1)}$$

where CAP is the cold-air potential in meters, z is the elevation of the location in meters above mean sea level, and $\min(z(d))$ is the minimum elevation within d meters of the location. Based on the local valley width, we set d to 500m.

Catkin phenology dates were converted to year-days (e.g., 2009-01-31 → 31 days) and then re-scaled for each tree for each year as follows:

$$cat2S_i = (cat2_i - \overline{cat2}) / (cat2_{last} - cat2_{first}) \quad \text{(Eq. 2)}$$

where, $cat2S_i$ is the re-scaled catkin day for tree i, $\overline{cat2}$ is the average day when catkin state 2 is first observed across all trees in that year, and $cat2_{last}$ and $cat2_{\text{first}}$ are the last and first dates when catkin state 2 is observed across all trees in that year, respectively. This value was averaged across years to estimate a tree's catkin phenology relative to other trees in the population.

We estimated each tree's phenological synchrony (S_i) with the rest of the population in each year as the proportion of trees producing pollen during the period when the tree bore female flowers. Specifically, for the period when a tree was in leaf state 2, we calculated the proportion of other trees that were in catkin state 3 or catkin state 4. Thus, S_i can range from 0 to 1, and can be averaged across all trees in a year to estimate population-level synchrony in a given year, or can be averaged across years for an individual tree to estimate that tree's mean synchrony with the population.

Acorn count data were averaged to estimate each tree's fecundity for the years 2009-2019 ($\bar{F}$). No acorns were observed on any trees in 2008 so we excluded that year from the analyses. In practice it made little difference whether 2008 data were included or not. For statistical analyses, the square root of mean counts was used to correct right skewness in the distribution of values.

To assess the association between timing of flowering, synchrony of flowering, and fecundity measures with environmental variables, we conducted OLS linear or polynomial regression analysis of pairwise relationships between variables. To test whether individual tree fecundity co-varied with synchrony, we calculated the correlation of synchrony and fecundity for each tree (93 trees after excluding 4 trees with consistently low production, 11 years). The average correlation for 93 trees was tested for non-randomness by comparing it to the distribution of values for 93 samples drawn from a N(0,1) distribution 1000 times.

Data exploration revealed strong association of fecundity with elevation, cold air pooling and geologic substrate. We used structural equation modeling (R statistical library, package **lavaan**) to isolate the direct effect of a tree's topographic position from its average pollination synchrony – which was indirectly related to topography due to the influence of cold air pooling on flowering phenology. To meet normality assumptions, mean acorn counts were square-root-transformed before analysis. Elevation was re-scaled by centering on the mean and dividing by the range in values. Synchrony scores were raised to the 5th power to address the strongly left-skewed distribution of that variable.

RESULTS

Correlation of phenology with acorn production

For the period 2008—2019, trees that flowered relatively early or late in the flower season tended to have lower fecundity (2nd order polynomial regression adj. $R^2 = 0.093$; df=2,94; $p = 0.004$; **Figure 2A)**. The relationship between fecundity and synchrony was weaker (linear regression, adj. $R^2 = 0.021$, $p = 0.08$; **Figure 2B**). Most trees had relatively high values of synchrony greater than 0.70 on a scale of 0-1, with the low synchrony levels being close to 0.50, indicating that the large majority of trees tended to produce female flowers when pollen was being released.

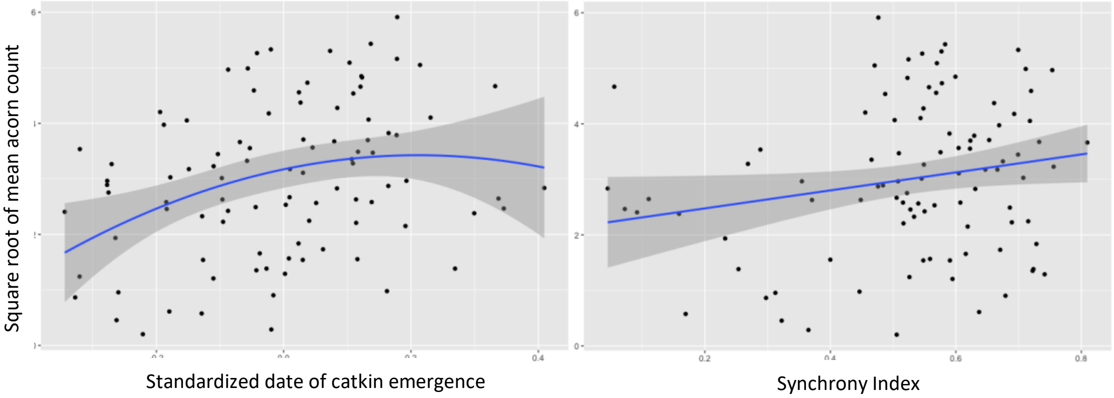

Figure 2. Relationship of catkin phenology to mean fecundity (**A**) and flower synchrony to mean fecundity **(B**) for 97 valley oaks, 2008-2019. Fitted lines are second order polynomial regressions, and shaded regions show pointwise 95% confidence intervals on the fitted values.

Correlation of environment, phenology, and fecundity measures

The timing of catkin emergence ranged widely between years, with median emergence date varying by more than a month from year-day 47 (late February) in 2014 to 84 (late March) in 2009 and 2019 (**Figure S1a**). Within any given year, first trees flowered 30 - 60+ days earlier than the last trees to flower. Timing of female flower appearance also varied by more than a month between years and between trees within years (**Figure S1b**). In any given year, phenology also ranged widely among trees; on average, early trees flowered more than a month before the latest-flowering trees (**Figure 2**). Importantly, individual trees were consistent from one year to the next in flowering earlier or later relative to the population as a whole (**Figure 3A**).

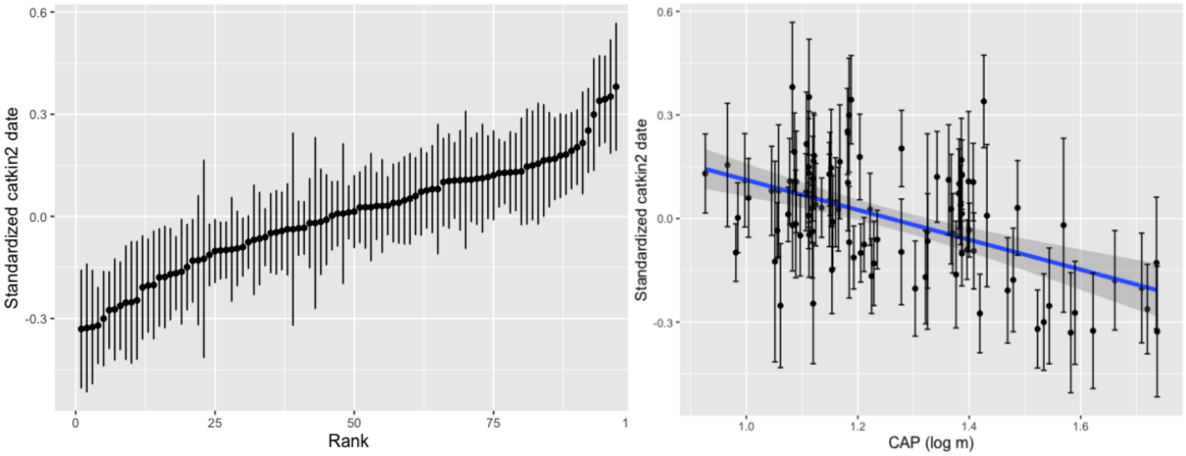

Figure 3. (A) Ranked means (dots) and standard deviations (vertical lines) of standardized catkin phenology scores for 97 trees, 2008-2019. On average, the earliest trees flowered more than a month earlier than latest-flowering trees. (**B**) Relationship between the cold air pooling index (CAP, eq. 1) and standardized catkin phenology (eq. 2) for 97 monitored trees (Adj. $R^2 = 0.25$; df = 1,95; $p < 0.001$). Fitted line is the linear regression, and shaded region shows pointwise 95% confidence intervals on the fitted values.

For trees whose temperatures were monitored, timing of catkin and female flower emergence were significantly related to January-April minimum and mean daily temperatures (**Table S1**). For the population as a whole, the average catkin stage 2 date advanced earlier by 10.6 days for every 1 °C increase in mean daily temperature of the January – April period (adj. $R^2 = 0.78$, df = 1,9; $p < 0.001$). Within any given year, tree-to-tree variation in catkin emergence was significantly related to thermal microclimate, specifically standardized minimum (adj. $R^2 = 0.26$; df = 1,43; $p = 0.0003$) and mean (adj. $R^2 = 0.19$; df = 1,41; $p = 0.002$) daily temperatures for the January-April period (**Table S1**). Variation in the appearance of female flowers also varied significantly with standardized minimum and mean daily temperatures (**Table S1**).

Local variation in measured daily temperatures was predicted with good skill by a tree's cold air pooling score, which explained 63% and 56% of inter-tree variation in minimum and mean daily temperatures, respectively (**Table S1**). Elevation alone explained 46% and 29% of the variation in minimum and mean temperatures, respectively (**Table S1**). Essentially, trees at lower elevations closer to the valley floor experienced significantly cooler daily minimum and mean temperatures. Accordingly, catkin and female flower phenology of 97 monitored trees was significantly related to both the cold air pool index and elevation (**Figure 3B, Table S1**).

Does flower phenology or environment predict acorn production?

As noted above, catkin phenology and flowering synchrony explained only 9% and 2% respectively of inter-tree variation in fecundity. Moreover, an individual tree's fecundity did not co-vary significantly with year-to-year variation in synchrony. The mean correlation of synchrony and fecundity for 93 trees was 0.019 ($p = 0.39$). Instead, the best predictor of a tree's fecundity was its relative elevation in the landscape (adj. $R^2 = 0.22$, df = 1,95, $p < 0.0001$).

In probing the association of fecundity with elevation, we found a negative relationship between tree size – specifically stem cross-sectional area at breast height – and relative elevation (**Figure S4**). This association led us to hypothesize that fecundity was more regulated by site water availability and/or edaphic conditions (**Figure S5A-E**). In short, valley oaks at higher elevations that are rooted in consolidated colluvium as opposed to deep alluvial fill presumably have less access to gravity water from downslope water movement and to the near-surface water table below the Figueroa Creek valley floor.

Given that microenvironment influences flower timing and acorn production and that flowering and acorn variables were correlated with several environmental variables (**Table S1**), we conducted a simple structural equation model to identify the most likely causal factors (**Figure 4**). The structural equation model indicates that relative elevation is directly and negatively related to fecundity and that a tree's synchrony – which is related to the cold air pooling index and thus indirectly related to elevation – bears only a weak positive relationship to fecundity (**Figure 4**, **Table 2**).

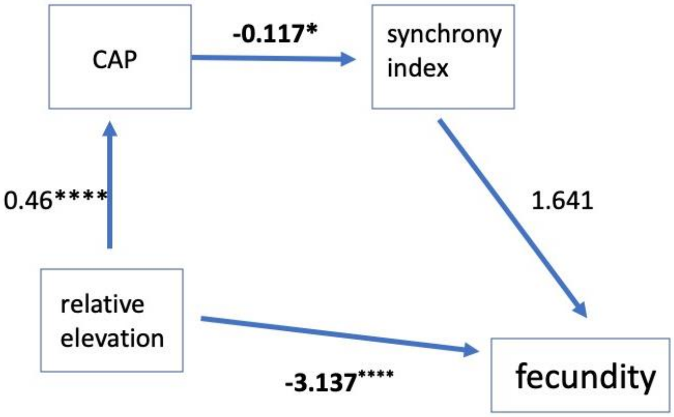

Figure 4. Directed path diagram representing the final results of the SEM relating a tree's elevation in the study area to its fecundity either directly or via pollination synchrony. Variables have been transformed to meet normality assumptions. Coefficients are for transformed variables. Asterisks indicate variable significance (* $p < -.10$, **** $p < 0.001$). See Table 2 for a summary of the model.

Table 2. Summary results of structure equation models (SEM) with 7 model parameters and 97 observations using Maximum Likelihood estimates. Only significant models are shown.

Dependent variable	Independent variable	Estimate	Std Err	Z-value	P (>| z |)
Regressions					
CAP	elevation	0.460	0.086	5.347	0.000
Synchrony	CAP	-0.117	0.06	-1.942	0.052
Fecundity	elevation	-3.137	0.603	-5.206	0.000
	synchrony	1.641	1.03	1.597	0.111
Variances					
CAP		0.029	0.004	6.964	0.000
synchrony		0.013	0.002	6.964	0.000
fecundity		1.389	0.2	6.964	0.000

DISCUSSION

Our study clearly shows that location matters. Microclimate and geomorphic position affect which trees flower when, which trees flower when other trees flower (Phenological Synchrony, S_i), and which trees produce the most acorns. Superficially, the fact that early and late flowering-trees produce fewer acorns **(Figure 1A)** implies that selection is favoring mid-season flowering and synchrony for mid-season flowering. This trend is very similar to that reported by (Koenig *et al.* 2012) for a population of valley oak in central California. In that study, the authors proposed that stabilizing selection is acting on flower phenology. In contrast, here we find that the timing of flowering is largely determined by each tree's thermal regime, which would reduce the heritability of the trait and dampen or eliminate a response to selection. More importantly, we also find weak evidence that the timing of flowering or the synchrony of flowering accounts for a tree's average acorn crop size. Instead, variation in acorn production appears to be far more regulated by site factors associated with soil and water supply.

Correlation of climate and phenology

The phenology of plants - including Mediterranean-climate oaks and valley oak in particular - is known to be regulated by temperature (e.g.,Badeck *et al.* 2004; Pinto *et al.* 2011; Koenig *et al.* 2015). Photoperiod is also an important control but not an exogenous source of variation at the local scale of our study. The timing of catkin emergence in our study population was well predicted using flowering season daily minimum or mean temperatures. Onset of catkin emergence ranged from late January to early March, with the female flowers emerging early and late in those same years but lagging by 10-30 days (**Figure S1 A, B**). The period of flowering for monitored trees lasted up to 60 days, implying that pollen was available for female flowers over a relatively long period. As a result, most trees had high phenological synchrony in most years. Such a long flowering period is not typical of all oaks and is probably affected by the rate of temperature change in spring. For example, the length of flowering season is shorter in Spain (e.g., 10-30 days, Bogdziewicz *et al.* 2020b) and is even shorter in Missouri, which has cold winters with temperatures that drop below freezing (Sork *et al.* 1993). By averaging fecundity of individual trees across many years, these differences in length of flowering season also get averaged out in our study and show that temperature may affect the timing of flowering but synchrony is not as important to fecundity

At our site, Intra-population variation in flower phenology was comparable in magnitude to interannual variation for the population as a whole, in this case due to fine scale variation in microclimate related to cold air pooling. The spatial pattern of cold air pooling was similar every year, so that the same trees flowered relatively early or late depending on their topographic position in the landscape. Trees at higher elevations produced staminate flowers early in the season and consequently bore female flowers at the time when many trees on the valley floor were producing pollen. In contrast, late-flowering trees in the coolest microsites bore female flowers at the very end of the season when one would expect pollen supply to be most limited. If acorn production was strongly dependent on pollen supply, one would expect fecundity to be lower at lower relative elevations in cooler microsites. In fact, we observed the opposite trend, although our sample included only a small number of very late flowering trees. Impacts of cold air pooling have been documented to produce landscape variation in phenology of other plant species (e.g., Fisher *et al.* 2006; Inouye 2008; Ward *et al.* 2018). The phenomenon is receiving heightened attention due to its potential role in buffering the impacts of climate warming (reviewed by Pastore *et al.* 2022).

Correlation of environment, phenology, and fecundity

Many factors are known to influence acorn crop size including endogenous factors, such as the age, health, and recent reproductive history of the tree (e.g., Sork *et al.* 1993) and exogenous factors, such as stand density, weather and water supply , weather during the flowering season, and drought (for a few of many examples, see Sork *et al.* 1993; Peter & Harrington 2002; Bogdziewicz *et al.* 2018; Puig-Gironès *et al.* 2023). In valley oak, acorn production in valley oak has been tied to flowering phenology, weather-related pollen supply, and water availability (Koenig *et al.* 1994b).

At our study site, fecundity increased at lower elevations in alluvium and presumably closer to the water table. Water availability may have been especially important between 2012 and 2016 when the region experienced extreme multi-year drought (Warter 2021). Overall, topographic position appears to exert more influence on fecundity than pollen limitation. Thus, the trend that early and late flowering trees have lower fecundity reflects the environmental impact on acorn production, which would reduce heritability of phenological synchrony and prevent stabilizing selection on synchrony. This finding contrasts with the often-cited conclusion of Koenig *et al.* (2012) that their valley oak population was under stabilizing selection on flower timing that would support the phenological synchrony hypothesis as an evolutionary driver of masting. We cannot dispute their claim, but we will point out that their similar trend could also be due to microenvironmental differences associated with tree location.

Our conclusions based on variation in phenology and fecundity for 98 trees across a 11-year period also contrast with the conclusions of Bogdziewicz *et al.* (2020b) who conducted an elegant pollen augmentation experiment during two reproductive seasons of *Quercus ilex* in an oak-savanna ecosystem in the Iberian Peninsula. In a study of 81 trees of an evergreen Mediterranean oak, *Q. Ilex,* Bogdziewicz *et al.* (2020b) found that the proportion of trees that flowered synchronously in a year with a shorter flowering season (10 days) resulted in more acorns than the asynchronous trees in a year with a longer flowering season (30 days). Importantly, their pollen augmentation treatment resulted in higher fruit set for the asynchronous individuals in the year with longer flowering interval, providing support for the hypothesis that phenological synchrony is a driver of masting. Their experimental findings certainly indicate that pollen limitation in asynchronous trees shapes fecundity. It would be interesting to know whether across years fine-scale environmental factors also shape the fecundity of individual trees.

Climate change and masting

One concern about the impact of climate on phenology is that climate change might disrupt flowering phenology across many plant species (Sherry *et al.* 2007; Augspurger & Zaya 2020). In an analysis of 39 years of seed production of a European Beech population (Bogdziewicz *et al.* 2020a), climate warming improved overall seed production but decreased year-to-year variation and reduced reproductive synchrony among individuals. This disruption of masting resulted in greater seed predation. In some oak species, climate warming may also affect masting, by reducing floral synchrony and seed production, (Bogdziewicz *et al.* 2020a) or by changing the masting intervals across years as modeled by Fleurot *et al.* (2023). Our findings suggest that other components of climate change such as increased drought and temperatures may affect masting by reducing the number of trees that produce acorns and reducing the size of the acorn crops in trees that do. Thus, Thus, the greater threat of climate change may be the stress on the fruiting stage.

Conclusions

In this population of valley oak, we find only weak evidence that phenological synchrony or pollen limitation are factors shaping acorn crop size. For trees like valley oak with long periods of flower availability, synchrony with other trees is extremely high and therefore pollen limitation is low. Instead, environmental factors associated with spatial location of the tree, most likely water limitation, determine fecundity. Thus, we conclude that phenological synchrony is unlikely to be a major driver of masting. Historically, other factors, such as predator satiation or resource limitation, that result in synchrony in flowering or fruiting across years are likely to have provided selection pressure favoring the evolution of masting. Looking forward, we are concerned that climate change may disrupt reproductive processes and reduce seed production of foundational tree species with negative cascading effects on the ecosystem.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

VLS designed the project; AL conducted field work; FD with VLS analyzed data; VLS and FD with input from AL wrote the manuscript.

PEER REVIEW

The peer review history for this article is available at [TBD]

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository through a temporary link: https://doi.org/10.5061/dryad.ghx3ffbvs

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Figure 3. (A) Ranked means (dots) and standard deviations (vertical lines) of standardized catkin phenology scores for 97 trees, 2008-2019. On average, the earliest trees flowered more than a month earlier than latest-flowering trees. (**B)** Relationship between the cold air pooling index (CAP, eq. 1) and standardized catkin phenology (eq. 2) for 97 monitored trees (Adj. $R^2 = 0.25$; df = 1,95; $p < 0.001$). Fitted line is the linear regression, and shaded region shows pointwise 95% confidence intervals on the fitted values.

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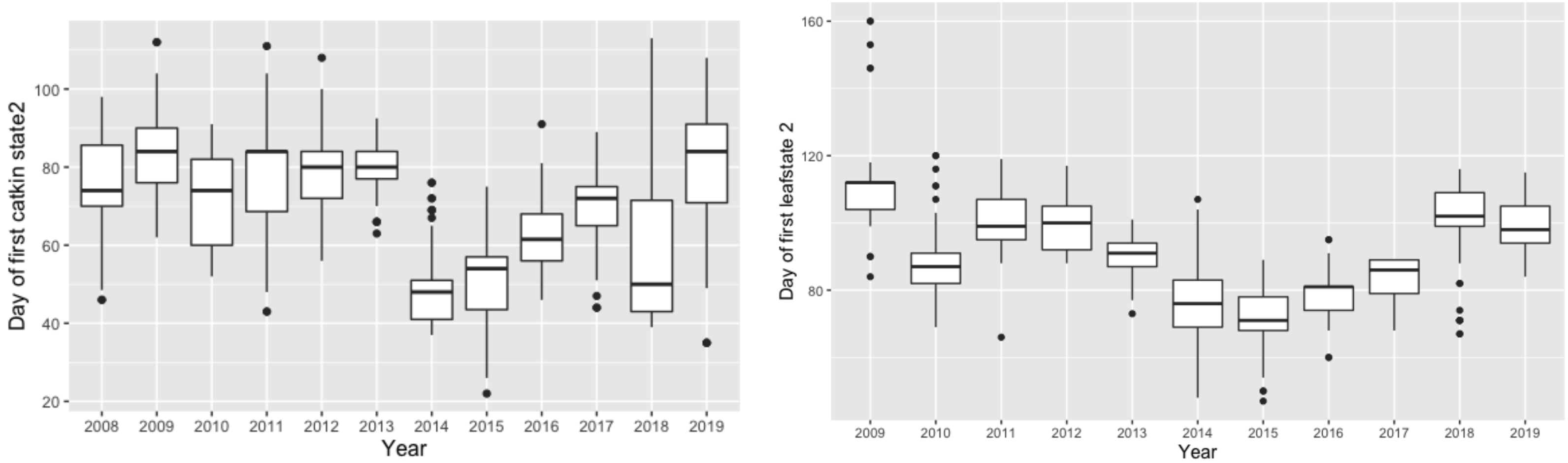

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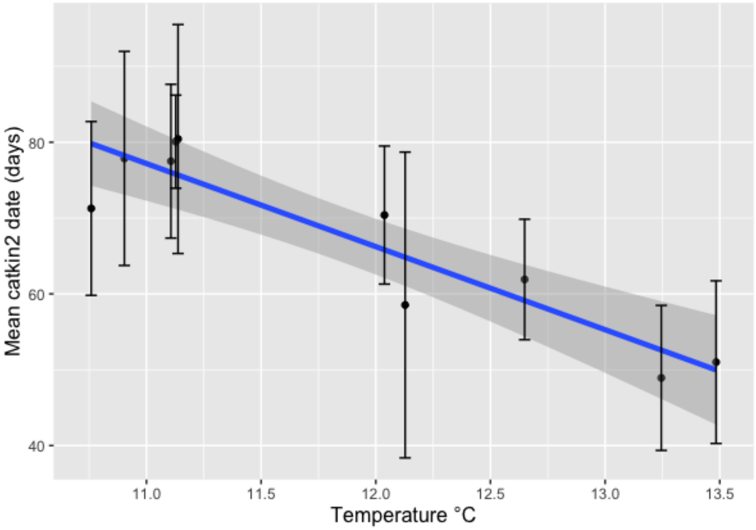

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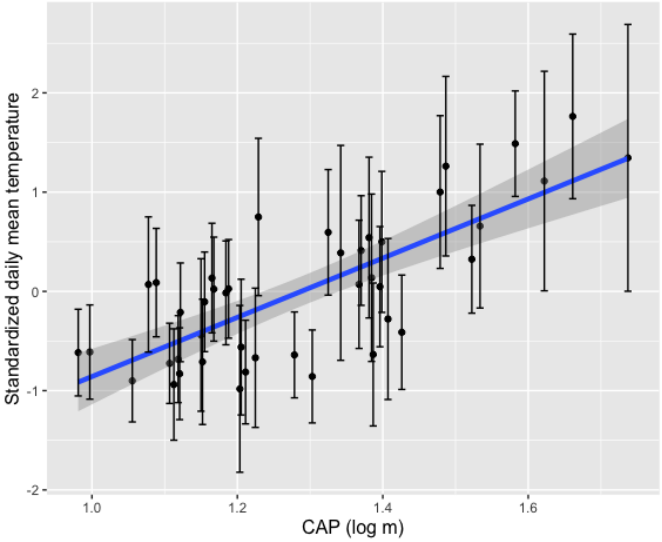
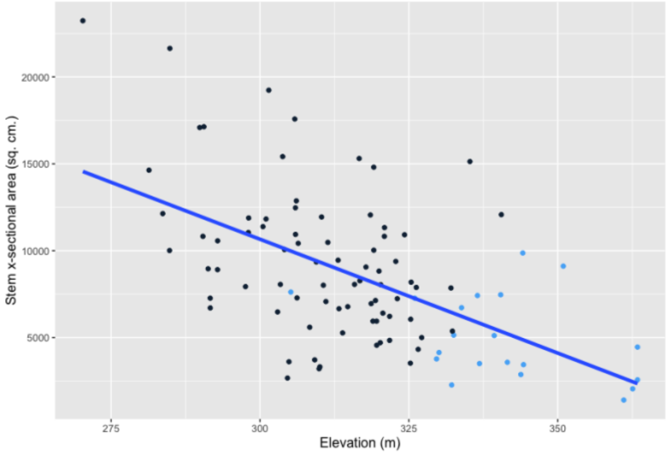


Figure S3. Relationship between CAP and standardized daily mean temperature for the flowering season for 43 monitored trees (Adj. $R^2 = 0.56$; df = 1,41; $p < 0.001$).



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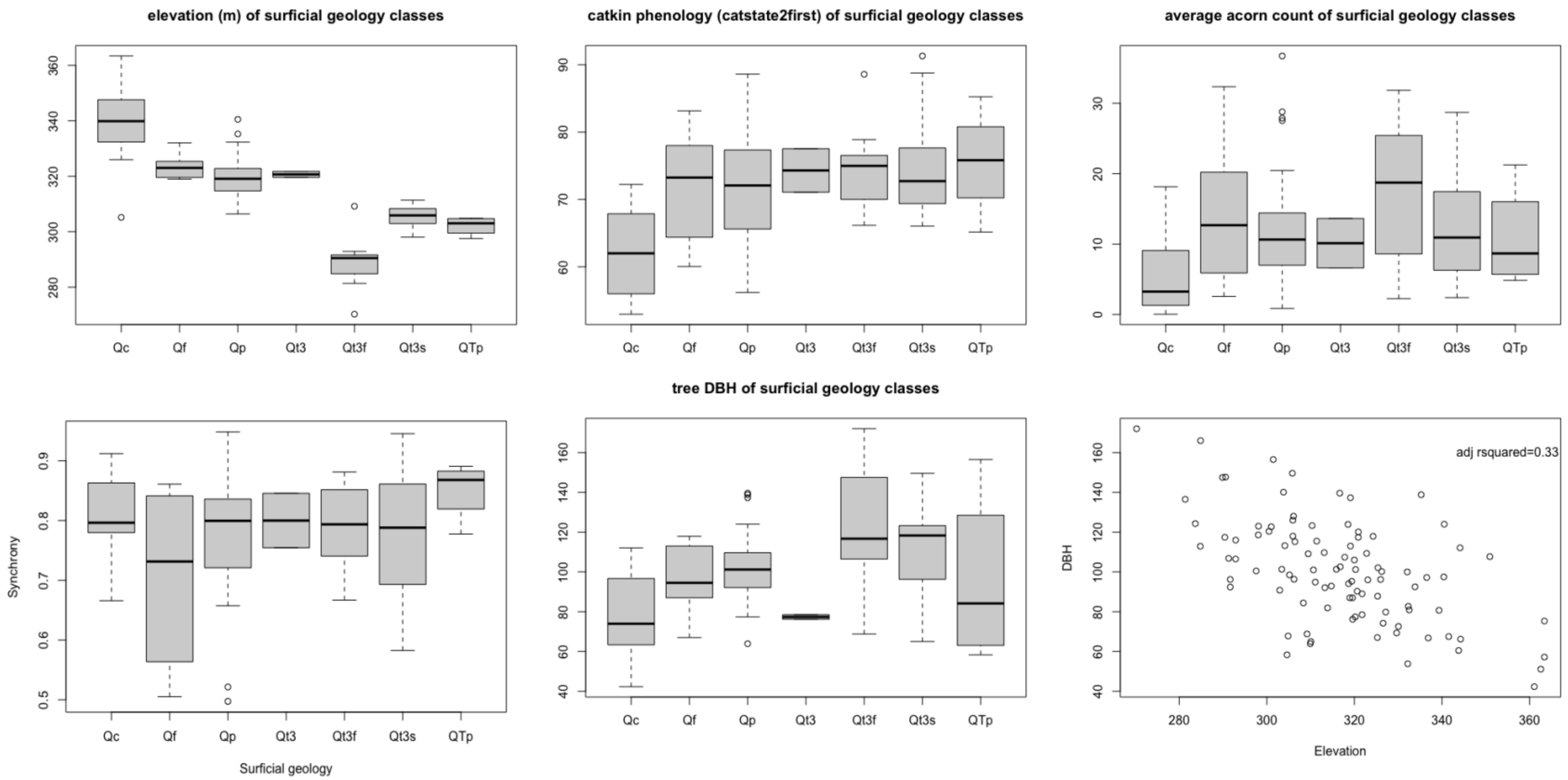

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Table S1. **Regression models.**

Analysis	**Dependent variable**	**Dependent variable**	**Y intercept**	**Slope**	**d.f.**	**Adj. R^2**	**F**
Inter-annual variation in population phenology vs temperature (2009-2019)	Average date of first catkin state 2	Mean January-April daily temperatures	193.224	-10.647	1,9	0.78	36.33****
Inter-tree variation in phenology vs temperature	Tree standardized catkin stage 2 score	Standardized minimum daily temperature, Jan-Apr	0.003	-0.120	1,41	0.26	15.53***
	Tree standardized catkin stage 2 score	Standardized mean daily temperature, Jan-Apr	0.002	-0.111	1,41	0.19	10.71***
	Tree standardized first leaf stage 2 score	Standardized minimum daily temperature, Jan-Apr	-0.003	-0.124	1,41	0.23	13.84***
	Tree standardized first leaf stage 2 score	Standardized mean daily temperature, Jan-Apr	-0.005	-0.109	1,41	0.17	8.63**
Measured temperature vs. temperature proxies	Standardized minimum daily temperature, Jan-Apr	Cold Air Pooling score	-4.316	3.360	1,41	0.63	72.63****
	Standardized mean daily temperature, Jan-Apr	Cold Air Pooling score	-3.841	2.983	1,41	0.56	53.98****
	Standardized minimum daily temperature, Jan-Apr	Elevation (m)	-8.538	0.027	1,41	0.46	37.85****
	Standardized mean daily temperature, Jan-Apr	Elevation (m)	-6.430	0.020	1,41	0.29	18.12***
Tree phenology vs. temperature proxies	Tree standardized catkin stage 2 score	Cold Air Pooling score	0.553	-0.439	1,95	0.25	32.97****
	Tree standardized leaf stage 2 score	Cold air pooling score	0.538	-0.427	1,95	0.20	24.85****
	Tree standardized catkin stage 2 score	Relative Elevation (m)	1.563	-0.005	1,95	0.30	41.37****

Analysis	**Dependent variable**	**Dependent variable**	**Y intercept**	**Slope**	**d.f.**	**Adj. R^2**	**F**
	Tree standardized leaf stage 2 score	Relative Elevation (m)	1.76	-0.006	1,95	0.32	46.19****
	Synchrony	Relative Elevation	0.798	-0.04357	1,95	-0.005	0.5295
	Synchrony	Cold air pooling score	0.000	-0.117	1,95	0.027	3.694*
Fecundity vs. environmental and phenological variables	Sqrt(average count)	Relative elevation	3.014	-3.2089	1,95	0.215	27.29****
	Sqrt(average count)	Cold air pool score	5.338	-1.845	1,95	0.059	7.006*
	Sqrt(average count) (2nd order polynomial)	Tree standardized catkin stage 2 score	3.0135	4.0133			
		(Tree standardized catkin stage 2 score)^2		-1.959	2,94	0.093	5.928***
	Sqrt(average count)	Synchrony^5	1.348	2.040	1,95	0.021	3.03*

Table S2. Correlation of flowering and fecundity variables with environmental variables. N = 97 trees, except for measured temperature variables (italicized), where N = 45. Temperatures are standardized mean daily values for the flowering season. (*** p < 0.001, **p < 0.01, * p < 0.05)

	Timing of catkin2	**Timing of first leaf state2**	**Timing of last leaf state2**	**Synchrony Index**	**Mean Acorn Count**	**Standardized acorn count**	***Min. temperature***	***Mean temperature***	***Max. temperature***	**Elevation**	**Cool Air Pooling Index**
Timing of catkin2	---										
Timing of fist leaf state 2	0.96***	---									
Timing of last leaf state2	0.91***	0.92***	---								
Synchrony Index	-0.27***	-0.29**	-0.20*	---							
Mean Acorn Count	0.25*	0.23*	0.23*	0.17	---						
Standardized acorn count	0.25*	0.23*	0.22*	0.15	0.99***	---					
Minimum temperature	-0.51***	-0.50***	-0.47**	-0.18	-0.50***	-0.49***	---				
Mean temperature	-0.44**	-0.39**	-0.40**	-0.20	-0.48***	-0.46**	0.92***	---			
Maximum temperature	0.09	0.09	0.01	-0.08	-0.03	-0.08	-0.09	0.28	---		
Elevation	-0.52***	-0.56***	-0.57***	-0.07	-0.40***	-0.37***	0.69***	0.55***	-0.24	---	
Cool Air Pooling Index	-0.49***	-0.45***	-0.50***	-0.19*	-0.18	-0.15	0.77***	0.68***	-0.07	0.48***	---