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Cues versus proximate drivers: testing the mechanism behind masting behavior

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Masting, the intermittent and synchronized production of seeds, is a common and important phenomenon throughout the plant kingdom. Surprisingly, the proximate mechanisms by which populations of masting plants synchronize their seed sets have been relatively unexplored. We examined how temperature influences the acorn crop of the valley oak *Quercus lobata*, a masting species common in California, USA, over 33 years in order to assess whether temperature acts directly on acorn crop as a cue or whether it acts instead through intermediate steps indicative of a direct mechanistic connection to acorn production. Compared to several alternatives, the difference in temperature during the spring flowering period over the prior two years (Δt) was a good predictor of annual acorn crop in valley oak, as proposed recently by Kelly et al. Significantly, Δt correlates positively with temperatures the previous April, a likely driver of pollination success in valley oak, and negatively with the previous year's acorn crop, which is in turn negatively correlated with the current year's acorn crop, presumably due to resource limitation. Thus, the success of Δt is not as a cue but rather explained by its close relationship to the proximate drivers that have a direct, mechanistic relationship with acorn crop size.

Masting, the intermittent and pulsed set of seeds, is a common and important phenomenon in many plant species (Silvertown 1980, Kelly and Sork 2002). Masting has been documented in diverse plant taxa ranging from temperate and tropical trees (Sork et al. 1993, Koenig et al. 1994b, Crawley and Long 1995, Curran and Webb 2000), to conifers (Koenig and Knops 2000, Sala et al. 2012), small legumes (Crone et al. 2009), various New Zealand trees, grasses and forbs (Schauber et al. 2002, Kelly et al. 2013), and even some agricultural seed crops (Rosenstock et al. 2011). Pulsed resources from masting events can have cascading ecosystem consequences (Ostfeld and Keesing 2000). For example, masting oaks in eastern North America influence ticks, tick-borne Lyme disease, gypsy moths and bird populations (Elkinton et al. 1996, Jones et al. 1998, Ostfeld and Keesing 2000, Schmidt and Ostfeld 2003).

Despite the considerable ecological importance of masting, it is still largely unknown how plant populations synchronize the effort they invest in reproduction at any one time (Kelly and Sork 2002). Two sets of observations have suggested that masting events are related to interannual patterns in weather. First, interannual variation in seed set in many taxa can be explained in part by variation in particular weather conditions (Sork et al. 1993, Koenig et al. 1996, Kelly and Sork 2002, Kelly et al. 2013). For example, a large acorn crop of valley oaks *Quercus lobata* in California correlates with warm temperatures early the prior spring (Koenig et al. 1996), and a high seed set of many New Zealand plants corresponds to years with warm temperatures the preceding summer (Schauber et al. 2002). Second, there is synchrony in masting at large geographic scales, making masting a prime example of the Moran effect. This suggests that weather, which is also synchronous at large spatial scales, is likely an important driver of masting behavior (Koenig and Knops 1998, 2013). While interannual weather patterns often correlate with seed set in masting plants, it is unknown whether such patterns are indicative of the proximate mechanism driving masting (the 'weather as a proximate diver' hypothesis), or if weather is a cue that plants use in order to synchronize seed crops (the 'weather as a cue' hypothesis) (Kelly and Sork 2002, Kelly et al. 2013).

The 'proximate driver' hypothesis suggests that weather affects seed set in masting species by directly impacting the processes by which seeds are produced: either flower production, pollination of flowers, the maturation of pollinated flowers, or some combination of the three. Evidence that weather operates on pollination or seed maturation has received support in several masting systems. For example, in the valley oak, warm spring temperatures result in greater synchrony of flowering among individual oak trees, which in turn result in greater seed production (Koenig et al. unpubl). Similarly, in New Zealand grasses, temperature is

a major driver of flowering time, which may affect seed set (Tanentzap et al. 2012). In the European *Quercus ilex*, experiments suggest that seed maturation is driven by interannual patterns of precipitation affecting the fruiting process (Perez-Ramos et al. 2010).

Other studies suggest that weather acts in concert with resource limitation in trees to produce patterns of masting (Koenig et al. 1996, Satake and Iwasa 2000). In particular, there is evidence that the seed set of plants is constrained by resource limitation resulting from the previous year's seed set. Indirect evidence includes a significant lag–1 negative autocorrelation in patterns of acorn production of several oak species (Sork et al. 1993, Koenig et al. 1994b). More directly, a high seed set reduced resource stores (in the form of carbohydrates) in whitebark pine *Pinus albicaulis* (Sala et al. 2012). Experimental evidence comes from a masting wildflower, where reduction in a given year's seed set increased seed production the subsequent year (Crone et al. 2009).

In contrast to the proximate driver hypothesis, the cue hypothesis suggests that weather, rather than having a direct impact on the success of a seed crop, is a reliable environmental cue that can be recognized by individuals over large spatial scales allowing them to benefit from the adaptive advantages of synchronized seed production (Kelly et al. 2013). This may be beneficial for those individuals, assuming that reproduction in years of population-level high seed set is advantageous. Several lines of evidence support this latter assumption, which is important whether masting is driven by proximate drivers or cues. First, the predator satiation hypothesis posits that per capita seed or seedling predation may be lower in masting years than in non-masting years, resulting in a fitness advantage for trees that set seed synchronously with others in the population (Janzen 1971, Perez-Ramos et al. 2008, Fletcher et al. 2010). Second, the seed dispersal hypothesis posits that seed dispersal agents are more effective in masting years than in non-masting years (Ims 1990). For example, in a tropical tree with pulsed seed set, scatter-hoarding rodents misplaced a greater proportion of cached seeds in high seed set years than in years with low seed set (Jansen et al. 2004).

Here we examine the proximate driver and cue hypotheses in the valley oak, a common wind-pollinated masting tree endemic to California. We focus on the hypothesis, recently proposed by Kelly et al. (2013), that a particular weather event, specifically the difference in temperature between two subsequent summers (Δt), is a conserved cue by which taxa synchronize their seed set. Our main goal is to test the Δt hypothesis and critically examine whether this weather pattern acts as an arbitrary cue, as proposed by Kelly et al. (2013), or whether its role is due to its underlying relationship with the proximate mechanisms driving variable seed production in this species. Specifically, the two proximate mechanisms potentially related to Δt in the system considered here are: 1) a direct effect of temperature the current spring (t_i) on subsequent acorn production, and 2) an indirect lagged effect of temperature the previous spring (t_{i-1}) on current acorn production due to its effects on acorn production the prior year affecting resource availability during the current year.

Methods

Site and weather data

Our study was conducted at Hastings Natural History Reservation, located 42 km southeast of Monterey, in central coastal California, USA. Hourly temperature has been recorded at this site throughout the study at a single location near the reservation headquarters. From these records we determined daily highs and monthly means. We focused on mean maximum April temperatures, as this has been shown to be the strongest correlate of acorn crops of this species in previous studies at the same site (Koenig et al. 1996).

Study system and data on acorn crops

Valley oak is a long-lived tree that is an important component of deciduous forests in central California. Due to low regeneration of young seedlings, however, populations of valley oak are considered at risk at our field site (Griffin 1971, Pearse et al. 2013) and across California (Tyler et al. 2006).

We measured the acorn crop of 84 valley oak trees at Hastings Reservation each September from 1980–2012 (33 years). For each tree, we estimated the acorn crop as the number of acorns counted in timed 15 s counts by two observers (Koenig et al. 1994a, b). These counts were summed (N30) and log transformed (LN30) in order to reduce the correlation between the mean and the variance. Even though acorn size varies in this system, acorn counts are a good measure of resource allocation to reproduction in *Q. lobata*, as there appears to be no tradeoff between acorn size and abundance (Koenig et al. 2009). In cases where we looked at the population-level acorn drop, the size of the annual acorn crop was estimated as the mean of the log-transformed counts for the 84 trees in the survey (xLN30).

Statistical analysis

Based on weather and previous acorn crops, we determined several predictors of the current acorn crop. First, we calculated the temperature the previous April (t_i) as well as the April temperature from the year before (t_{i-1}). From these variables, we calculated the temperature difference [April temp (t_i) – April temp (t_{i-1})], hereafter Δt, after Kelly et al. (2013). In addition, we used the acorn crop from the previous September ($N30_{i-1}$) as a predictor of the current acorn crop.

Because the effect of nutrient limitation based on previous acorn production should be within trees, we conducted analyses at the level of the individual tree. In order to compare directly with Kelly et al. (2013), we also conducted analyses at the population level. In all but one analysis the results were qualitatively identical, and thus we report only the individual-based analyses except for the case where results differed, where we report results of both analyses.

We constructed a series of mixed models where temperature and/or previous acorn crop predicted a current

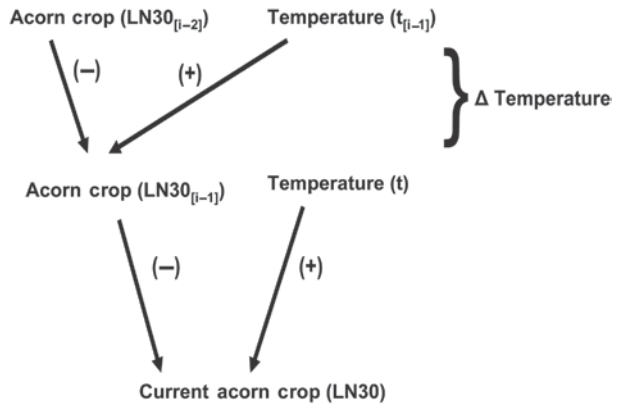

Figure 1. A conceptual diagram showing expected relationships between weather, acorn crop, and previous seed set. Numerous studies have demonstrated a correlation between warm seasonal weather and seed set, likely due to the influence of weather on either pollination or seed development. Likewise, resource limitation due to a high previous acorn crop has often been shown to reduce subsequent seed set in several masting species. At the same time, a recent study has suggested that the difference in temperature between years is a good predictor of seed set for a number of taxa. We propose that the effect of temperature difference (Δt) is mediated through the direct effects of recent weather and the effect of previous weather via previous seed set. Alternatively, Δt may act as a cue for seed set independently of the processes described above.

year's acorn crop with 'tree' as a random factor. First, we asked whether Δt was a better predictor of the acorn crop than the temperature of either the previous April (t_i) or that of the year before (t_{i-1}). Similar to Kelly et al. (2013), we compared the predictive value of four models on acorn crop using AIC (Burnham and Anderson 2002): 1) previous April temperature (t_i); 2) temperature of the April before (t_{i-1}); 3) Δt, and 4) both previous April temperature and the temperature from the year before (referred to by Kelly et al. 2013 and subsequently as the '2t' model).

Next, we explored the proposed mechanistic links between weather and the acorn crop (Fig. 1). Our first model included the expected negative autocorrelation between the previous acorn crop and the current acorn crop. Next we explored the correlations between Δt and 1) the previous acorn crop, 2) April temperatures the prior spring (t_i), and April temperatures the prior year (t_{i-1}). Finally, we constructed a regression model to predict the acorn crop based on the mechanisms proposed in Fig. 1. Using a likelihood ratio test, we compared this model, in which the acorn crop is determined by the previous April temperature through its proposed effect on pollen limitation and the size of the previous acorn crop as a proxy for resource limitation, to an identical model that also included Δt, in order to assess whether Δt explained variation in acorn crop that could not be explained by the two proposed mechanisms.

Analyses at the individual level were conducted as linear mixed models; the one analysis we report on that was done at the population level employed a linear model. All statistics were calculated in R 2.10.1 using the package nlme (Pinheiro et al. 2009).

Table 1. Comparison of predictors of *Q. lobata* acorn crop. Where t_i is spring temperature, t_{i-1} is the temperature of the previous spring, and Δt is the difference in temperature between the past two springs. Mixed models were constructed with 'tree' as a random factor.

Predictors	ΔAIC	R^2	p
2t (t_i, t_{i-1})	0	0.49	<0.001
Δt	97.8	0.47	<0.001
t_i	248.6	0.44	<0.001
t_{i-1}	810.8	0.30	<0.001

Results

The predictive value of Δt on seed set

The 2t model (ΔAIC = 0) was more predictive of acorn crops than models that included only t_i, t_{i-1}, or the combined Δt measure (Table 1). As a single factor, however, Δt explained a slightly higher proportion of variation in the acorn crop than temperature of the previous April alone, although both were highly significant (Fig. 2).

A mechanistic explanation relating Δt and masting

Consistent with the hypothesis of resource limitation, there was a negative correlation between the current year's acorn crop ($N30_i$) and the acorn crop the previous year ($N30_{i-1}$)

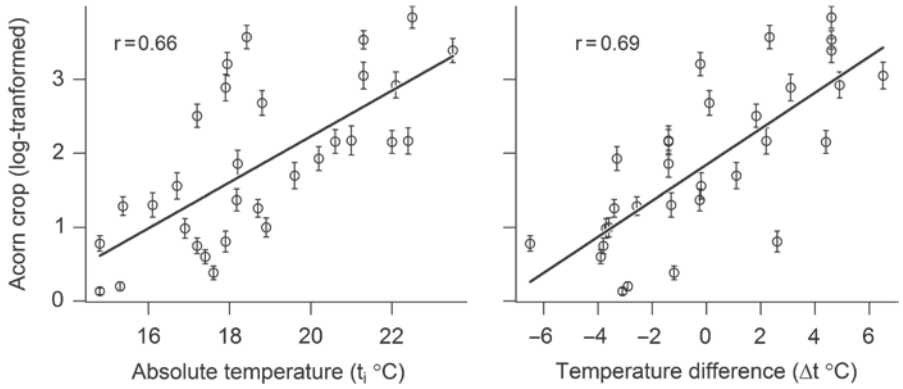

Figure 2. The predictive value of temperature from the previous spring t_i and the difference in temperatures between the previous two springs (Δt) on a year's acorn set in *Q. lobata* over 33 years of acorn censuses. Error bars represent standard errors. The trendline is from a mixed model regression.

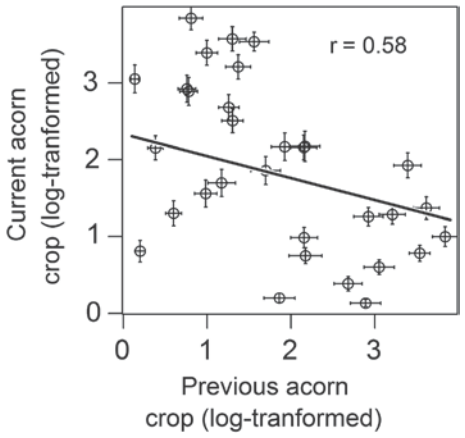

Figure 3. The negative correlation between a current year's acorn crop, and the previous year's acorn crop ($N30_{i-1}$). Error bars represent standard errors. The trendline is from a mixed model regression.

($r = -0.54$, $p = 0.001$, Fig. 3). Further, there was a negative correlation between Δt and the previous year's acorn crop ($r = -0.76$, $p < 0.001$, Fig. 4a). As expected given its composite nature, Δt incorporates, and is therefore positively correlated with, t_i ($r = 0.65$, $p < 0.001$, Fig. 4b), and negatively correlated with t_{i-1} ($r = -0.65$, $p < 0.001$, Fig. 4c).

We constructed an individual-level mixed model that included the two components of our hypothesized mechanistic model of acorn masting: previous April temperature, which has a potential direct effect on pollination; and the previous year's acorn crop as a proxy for resource limitation (Table 2). These two parameters explained 54.1% of the variation in acorn crop ($F_{2,28} = 18.7$, $p < 0.001$). Inclusion of Δt in this model improved the prediction of the acorn crop (log-ratio = 165.8, DF = 1, $p < 0.001$). Since t_i was already included in the model, this indicates that the additional support provided by Δt in this analysis is due to an effect of conditions the prior spring that is in addition to its importance as a proxy for resource limitation (Fig. 1). In contrast, the inclusion of Δt failed (barely) to significantly improve a model using current temperature and resource limitation to predict acorn masting in the population-level analysis ($F_{1,27} = 3.97$, $p = 0.06$).

Discussion

We found that the best-supported model of a given year's acorn crop of valley oaks at Hastings Reservation was one that included both early spring temperature the year of and early spring temperature the year before the acorn crop matured in the fall. However, the difference in temperature between the prior two springs (Δt) was the best single weather-related predictor of a given year's acorn crop in valley oaks at Hastings Reservation, supporting the conjecture of Kelly et al. (2013) that this variable is a strong correlate of masting behavior.

This result does not, however, address the key question of whether Δt acts merely as a cue or whether its strong performance is because it encapsulates key features related to mechanisms directly affecting seed production. Based on the

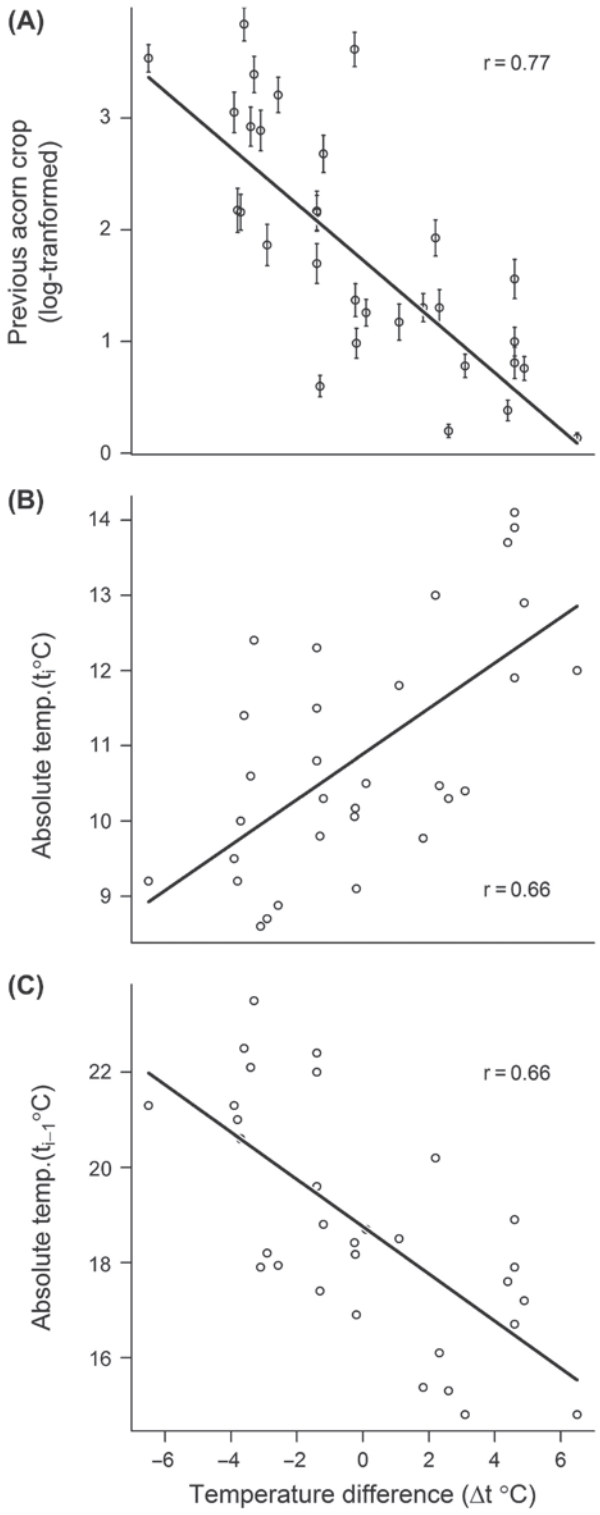

Figure 4. Covariation between the difference in temperatures between the previous two springs (Δt) and explanatory factors of acorn production. (A) The negative correlation between Δt and the previous year's acorn crop ($N30_{i-1}$) in *Q. lobata*. (B) The positive correlation of Δt and temperature the prior spring (t_i). (C) The negative correlation between Δt and temperature during the previous year's spring (t_{i-1}).

relationships between current and prior acorn production as well as current acorn production and spring conditions, our data support the latter (the weather as a proximate driver

Table 2. Comparison of mechanistic models with and without temperature difference. The first model includes our proposed proximal drivers of acorn production: previous acorn crop and previous spring temperature. The inclusion of temperature difference (Δt) significantly improved the model. As current temperature is also included in this model, all of the additional effect of Δt is attributable to the previous year's temperature.

Model	AIC	Likelihood ratio	p
Current acorn crop ($LN30_i$) ~ prior year's acorn crop ($LN30_{[i-1]}$) + current spring temperature (t_i) + Δt	9006	165.9	<0.001
Current acorn crop ($LN30_i$) ~ prior year's acorn crop ($LN30_{[i-1]}$) + current spring temperature (t_i)	9182		

hypothesis). Specifically, we showed that potential causal links connect Δt with the acorn crop in valley oaks. When Δt is high, this necessarily means that either the previous April temperatures were high or the temperatures of the April the year before were low. High temperatures in April increase the synchrony of flowering in oaks, which results in greater acorn crops the subsequent fall, presumably because of greater pollination success (Koenig et al. unpubl). High temperatures the previous April affect the previous year's acorn crop in a similar manner, so t_{i-1} positively correlates with the previous year's acorn crop ($N30_{i-1}$). There is a negative autocorrelation between the current year's acorn crop ($N30_i$) and the previous acorn crop ($N30_{i-1}$), most likely being driven by resource limitation (Crone et al. 2009, Sala et al. 2012). Thus low April temperature the prior year correlates with increased current acorn production (Fig. 1).

Kelly et al. (2013) argued that the effect of Δt on seed production was more parsimoniously considered an arbitrary cue than as an effect representing proximate drivers. There are at least two problems with this hypothesis. First, the suggestion that Δt acts merely as a cue is a null hypothesis that cannot be directly tested. It can, however, be rejected by evidence indicating that Δt is a proxy for specific mechanisms directly affecting acorn production. We provide such evidence here in the case of the valley oak. Second, a proximal effect of weather on acorn production via pollination success and resource limitation is in fact simpler and more parsimonious than the hypothesis that Δt acts as a cue. Response to Δt as a cue requires the ability to perceive and remember the cue (in this case temperatures during a specific time period integrated over a two year period) and respond accordingly (in this case produce an appropriately-sized acorn crop) (Karban 2008). No mechanism by which plants could successfully accomplish these two phenomena, particularly that of remembering temperatures over a two-year period, is currently known. We consider it far more likely that patterns of masting, both in valley oak and other species, are generally driven by specific mechanisms influencing the production of flowers, resource availability, or both, in many if not all cases mediated through specific environmental factors such as temperature and/or rainfall.

Thus, our data supports the weather as a proximate driver hypothesis. We found that the proposed arbitrary cue (Δt) correlated strongly with previous acorn set and current weather conditions that affect pollination (Fig. 4). Interestingly, however, we found that a model that represents our current understanding of the mechanisms driving the size of the acorn crop in valley oaks was still improved by the inclusion of Δt as an additional explanatory factor, at least when analyzed at the individual tree level. This suggests that the effect of the prior year's spring temperature (a component of Δt) on the current acorn crop is not entirely mediated by resource limitation due to the previous year's acorn crop.

This result is not surprising given the numerous other mechanistic factors by which previous temperature could affect the seed crop. First, the physiological determination of reproductive tissues in oaks occurs the year prior to floral development (Merkle et al. 1980). Consequently, weather events the previous year could affect subsequent investment in flowers, which could in turn result in differences in seed set. Alternatively, spring temperatures or other environmental factors are likely to affect other forms of resource storage. Colder springs in California, for example, may correspond to greater rainfall, and with greater rainfall in a previous year, more resources are likely to be available for subsequent acorn production. While rainfall does not directly affect acorn production in valley oaks, it has been shown to affect the tradeoff between current and subsequent reproduction (Barringer et al. 2013). Indeed, while temperature explains 49% of the variation in seed set of valley oak between years (Table 1), there are also complicated life history trade-offs involving trunk growth, leaf production, and water retention that may account for additional variation in seed set (Barringer et al. 2013).

There are a wide range of weather patterns that correlate with masting in various different systems. For example, summer temperature, spring temperature, and rainfall each explain variation in masting in the seed set of different tree species (Koenig et al. 1996, Schauber et al. 2002, Perez-Ramos et al. 2010). Nevertheless, one commonality among these systems is that the weather conditions the previous year are plausibly related to current seed set via fertilization success or resource limitation. Indeed, while the weather correlates of acorn production in other oaks are not always the same as for valley oak (Koenig et al. 1996), there is evidence for a negative correlation between current and subsequent reproduction in most of these systems (Barringer et al. 2013). Thus, models that incorporate weather from the previous two years should be strong predictors of seed set. This is not, however, because the variables involved are cues, but rather because they are proxies for mechanistic factors directly affecting seed production.

One major consequence of this is that climate change will potentially have significant effects on masting patterns, contrary to the conclusion reached by Kelly et al. (2013) proposing that weather acts solely as a cue. This is especially true in valley oak, where evidence suggests that masting is driven by differences in flowering synchrony driven in turn by annual differences in microclimatic variability correlated with overall spring temperatures (Koenig et al. unpubl.). Evidence for changes in masting driven by global climate change will potentially require long-term data to detect and remain to be detected. In line with the weather as a proximate driver hypothesis, however, we predict that such evidence will be forthcoming.

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