



# Acorn Production and California Oaks in a Changing World

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## ABSTRACT

How are oaks responding to a changing world? At Hastings Reservation in central coastal California, conditions have warmed an average of 1.08 °C over the past 80 years, primarily due to increasing temperatures at night over much of the year. These changes appear to have had no detectable effect on acorn production by any of the five species at this site. However, variability in acorn production – mast behavior – has decreased considerably since 1980, the first year for which data are available. This decrease is matched by decreased variability in annual rainfall over the same 39-year period, although over a longer, 80-year period the trend in variability of annual rainfall has been positive rather than negative. Even more dramatic effects on oak populations have been apparently due to changes in land use. In particular, canopy cover at Hastings increased from 22.2% to 42.7% between 1979 and 2013. This was primarily due to increased density of *Quercus agrifolia*, the main evergreen species, at the expense of the deciduous *Q. lobata*, a pattern that is found elsewhere in California as well. Understanding changing oak populations and protecting them in the future will require careful consideration of multiple factors, including climate change, land-use patterns, and other ecological factors such as interspecific interactions that will potentially be even more difficult to detect and interpret.

**Keywords:** acorn production, climate change, land-use patterns, oak communities

## Introduction

The only constant in the world is change. This truism has received particular attention in recent years due to the unprecedented rate of climate change that has already affected many populations (Walther et al. 2002) and is expected to impact many more in the future, including oaks. Complicating our understanding of climate change is that its effects vary greatly not only geographically but on a local scale, particularly in heterogeneous landscapes such as California. As a result, focusing on individual sites is critical if we are to take into account variability in the potential effects of climate change over larger geographic scales.

One such site is Hastings Natural History Reservation (hereafter "Hastings"), a field station located in central coastal California approximately 40 km from the coast. Hastings was established in 1937 and has been a center for oak research since the 1960s, with early work by Keith White (1966) and James Griffin (1971), and, more recently, Pam Muick (1991), Ray Callaway (1992), and others. My own ongoing oak work has focused on acorn production and extends back to 1980.

My goal here is first to quantify environmental changes that have taken place at Hastings since its founding in order to assess the extent of climate change at this site. Next I look at patterns of acorn production in order to identify whether any trends are evident, and if so, whether they are in accord with environmental changes. I look at both the size and variability of the acorn crop – the latter being the degree of masting behavior. Whether masting is likely to be affected by climate change is controversial, depending largely on the proximate mechanism driving annual variability (Pearse et al. 2016). Finally, I discuss the vegetation changes that have taken place at Hastings since its founding due to changes in land use.

## Methods

Weather data (daily maximum and minimum temperature and rainfall) has been taken continuously at Hastings headquarters since 1937. Hastings experiences a Mediterranean climate, with the vast majority of rain falling between October and April. Thus, data were analyzed by fiscal year (July through June).

Data on acorn production come from visual surveys conducted annually since 1980 on 250 mature trees of five species, including *Quercus lobata* (valley oak;  $N = 86$ ), *Q. douglasii* (blue oak;  $N = 56$ ), *Q. agrifolia* (coast live oak;  $N = 63$ ), *Q. chrysolepis* (canyon live oak;  $N = 21$ ), and *Q. kelloggii* (California black oak;  $N = 20$ ). Two observers scanned different parts of each tree and counted as many acorns as possible in 15 s; these counts were added to yield acorns per 30 s ("N30"). For analyses of variability, values were  $\ln$  transformed ( $\ln(N30+1)$ ). Further details are available in Koenig et al. (1994a, b).

Vegetation surveys were conducted in 1979 and repeated in 2013 using a modification of the 0.04 ha circular plot protocol of James and Shugart (1970). Samples were taken at 613 sample grid cells covering approximately 230 ha of oak habitat. Within grid cells, we recorded the diameter at breast height (DBH) and the species of all trees that were  $>1$  m in height. From this, basal area was estimated. Further details are presented in McMahon et al. (2015).

Analyses were conducted in R3.3.1 (R Core Team 2016).

## Results

### Weather

Data for mean temperature and rainfall (Fig. 1) illustrate the considerable annual variability typical of Mediterranean climates, particularly of rainfall. Also noteworthy is that rainfall is not normally distributed. Rather, the data are highly left skewed, with 50 of 79 years (63%) experiencing rainfall below the mean.

Over the 80-year period for which data are available there has been no significant change in either mean maximum temperature or annual rainfall (Fig. 1). Mean minimum annual temperature, however, has increased  $0.0135^{\circ}\text{C year}^{-1}$ , for a total estimated increase

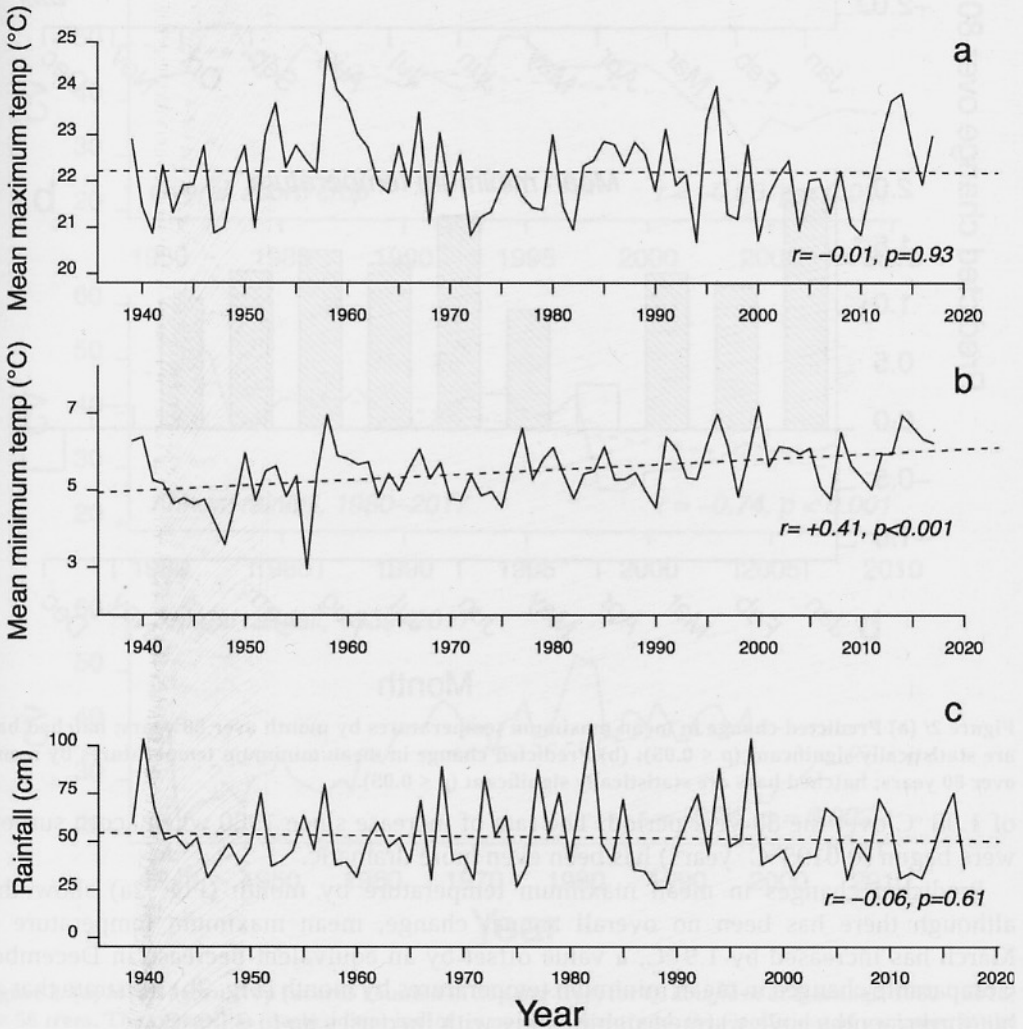


Figure 1/ Annual (a) mean maximum temperature; (b) mean minimum temperature; and (c) total rainfall at Hastings Reservation. Data are for fiscal years (July through the following June), 1937-38 to 2017-18. Solid lines connect the annual values; dashed lines are the regressions. Pearson correlations and their p-values are listed; only the regression for time on mean minimum temperature is significantly different from zero.

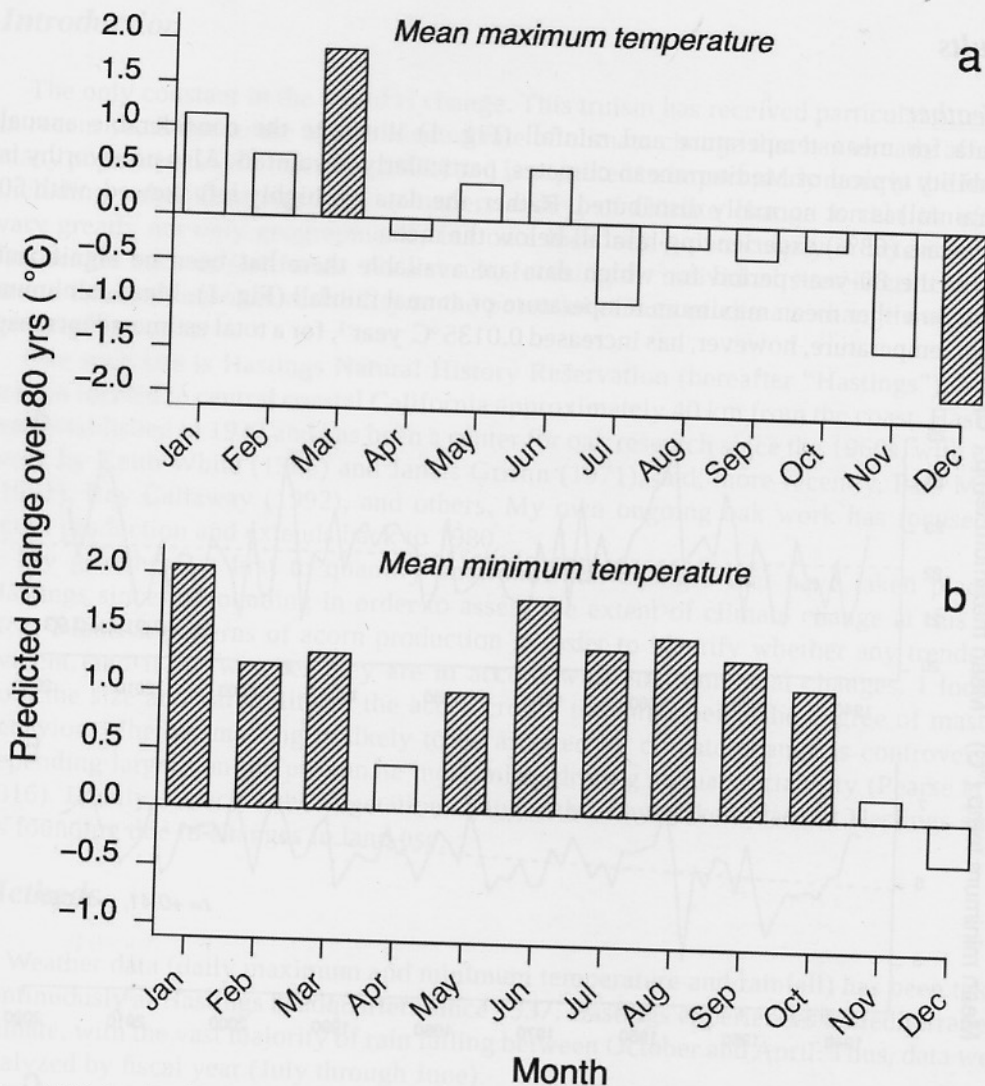


Figure 2/ (a) Predicted change in mean maximum temperatures by month over 80 years; hatched bars are statistically significant ( $p < 0.05$ ); (b) Predicted change in mean minimum temperatures by month over 80 years; hatched bars are statistically significant ( $p < 0.05$ ).

of 1.08 °C over the 80-year period. The rate of increase since 1980 when acorn surveys were begun ( $0.0195\text{ }^{\circ}\text{C} \cdot \text{year}^{-1}$ ) has been even more dramatic.

Predicted changes in mean maximum temperature by month (Fig. 2a) show that although there has been no overall annual change, mean maximum temperature in March has increased by 1.9 °C, a value offset by an equivalent decrease in December. Comparable changes in mean minimum temperatures by month (Fig. 2b) illustrate that all but three months have warmed significantly with increases up to 2.06 °C.

#### Acorn production

There have been no significant trends in mean acorn production by any of the five species surveyed ( $-0.17 < r < 0.06$ , all  $p > 0.3$ ). As an example, data for *Q. douglasii* is graphed (Fig. 3a).

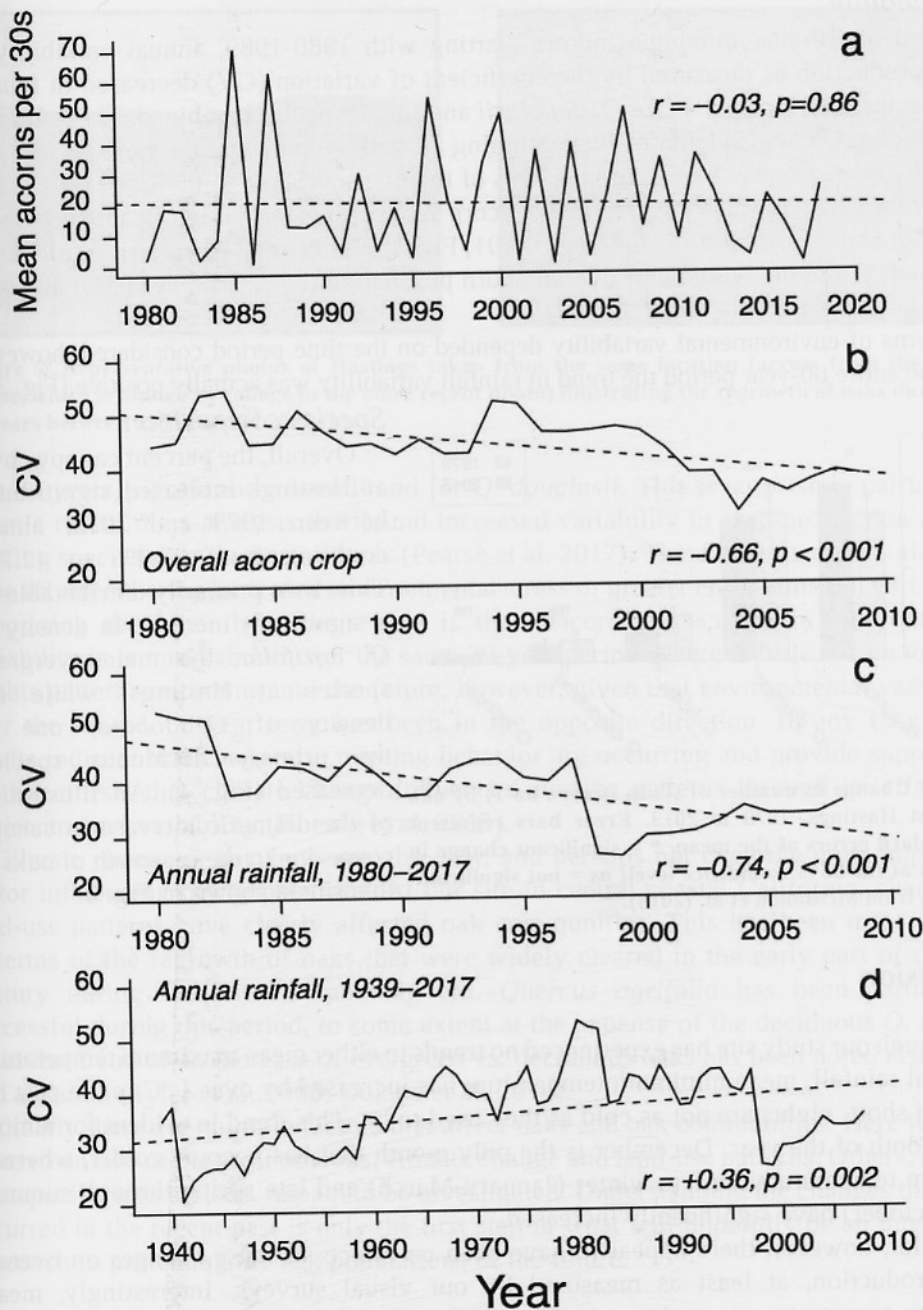


Figure 3/ (a) Mean acorn crop (acorns counted in 30 s per tree) for *Q. douglasii* at Hastings, 1980 – 2018;  $n = 56$  trees. The regression (dashed line) indicates no temporal trend. (b) Coefficient of variation in the mean ( $\ln$ -transformed) acorn crop of all five oak species combined based on 10-year moving averages, 1980-1989 to 2009-2018. The regression (dashed line) indicates a strong negative trend in CV over time. (c) Coefficient of variation in annual rainfall based on 10-year moving averages, 1980-1989 to 2009-2017. The regression (dashed line) is drawn. (d) Coefficient of variation in annual rainfall based on 10-year moving averages, 1939-1940 to 2009-2017. Note the positive regression (dashed line), in contrast to the pattern observed when analyzed starting in 1980-1989.

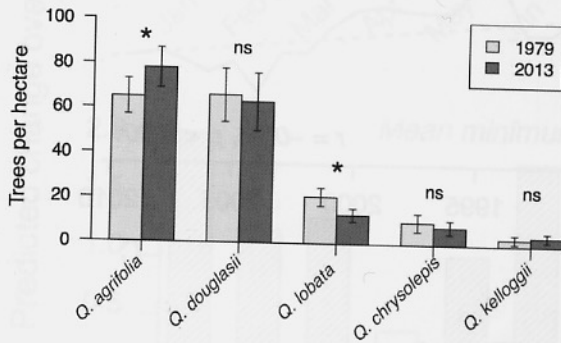


## Variability

Based on 10-year moving windows starting with 1980-1989, annual variability in acorn production as measured by the coefficient of variation (CV) decreased in four of five species, significantly so for *Q. douglasii* and for all species combined. The latter was true whether CV was calculated by combining all individuals regardless of species (Fig. 3b) or by averaging (within years) the CVs of the five species ( $r = -0.48$ ,  $p < 0.01$ ).

Over the same 39 years covered by the acorn survey there was a significant decrease in the CV of annual rainfall ( $r = -0.74$ ,  $p < 0.001$ ; Fig. 3c). This trend correlated significantly with the CV moving window of overall acorn production ( $r = +0.37$ ,  $p = 0.05$ ) and with that of *Q. douglasii* ( $r = +0.47$ ,  $p = 0.01$ ).

Patterns of environmental variability depended on the time period considered, however. Over the entire 80-year period the trend in rainfall variability was actually positive (Fig. 3d).



**Figure 4/** Change in number of stems (trees . ha<sup>-1</sup>) by oak species at Hastings, 1979 to 2013. Error bars represent two standard errors of the mean. \* = significant change in the mean at the 95% confidence level; ns = not significant. Redrawn from McMahon et al. (2015).

## Species composition

Overall, the percent canopy cover at Hastings increased significantly between 1979 and 2013, almost doubling from 22.2% to 42.7%. This was primarily attributable to a significant increase in density of *Q. agrifolia*, the main evergreen species at Hastings, while the density of *Q. lobata*, one of the primary deciduous species, decreased (Fig. 4). An illustration of the dramatic increase in canopy cover due to the regrowth of oaks at this site is shown in Fig. 5.

## Discussion

Although our study site has experienced no trends in either mean maximum temperature or annual rainfall, mean minimum temperature has increased by over 1 °C in the past 80 years. In short, nights are not as cold as they used to be. This trend is evident for almost every month of the year. December is the only month that has become colder, whereas minimum temperatures in late winter (January-March) and late spring through summer (May-October) have significantly increased.

Thus far, however, there appear to have been no effects of these changes on overall acorn production, at least as measured by our visual surveys. Interestingly, mean maximum temperature in early spring – specifically during April – has a particularly strong correlation with subsequent acorn production in several of the key species in our study site (Koenig et al. 1996). Given that there has been virtually no change in mean maximum April temperature (Fig. 4), the lack of any trend in overall acorn production is perhaps unsurprising. Whether increasing temperatures during other times of the year will eventually affect resources in a way that impacts overall acorn production remains to be seen.

In contrast, variability of acorn production – masting behavior – has decreased over the

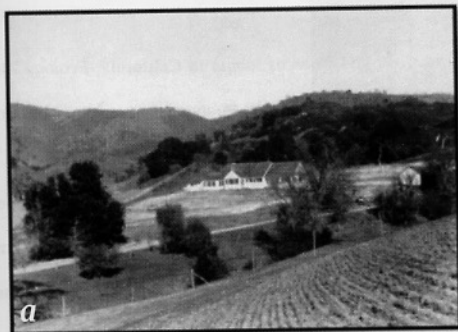


Figure 5/ Representative photos of Hastings taken from the same location (across from the School House, which is hidden by foliage in the more recent photo) illustrating the regrowth of oaks during the 71 years between 1931 (a) and 2002 (b).

past 39 years, significantly overall and for *Q. douglasii*. This is surprising, particularly given a recent meta-analysis that found increased variability in seed production among masting species over the past century (Pearse et al. 2017). This finding was hypothesized to be driven either by increased environmental stress or greater environmental variability. Supporting the latter hypothesis here is the concordant decrease in environmental variability in annual rainfall over the same 39-year period. There is little reason to count on this pattern continuing into the future, however, given that environmental variability over the longer, 80-year term has been in the opposite direction. In any case, these results indicate that changes in masting behavior are occurring and provide support for the hypothesis that climate change influences masting patterns through its effects on environmental variability (Koenig et al. 2015).

Climate change is not, however, the only, and perhaps not even the most important, factor influencing oak populations. At our site in central coastal California, changes in land-use patterns have clearly affected oak communities. This has been most evident in terms of the regrowth of oaks that were widely cleared in the early part of the 20<sup>th</sup> century during California's ranching era. *Quercus agrifolia* has been particularly successful during this period, to some extent at the expense of the deciduous *Q. lobata*. A similar trend of an increase of evergreen vs. deciduous oaks has been noted elsewhere in California (Tyler et al. 2006; Dolanc et al. 2014).

Clearly there are multiple factors that affect oaks and oak communities. Here we have focused on two of the most obvious, climate change and land-use patterns. Others, such as interspecific interactions, remain to be investigated. Understanding the changes that have occurred in the recent past is only the first step in what will hopefully be an integrative approach to protecting the oak populations of the future.

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**Photographers.** Title page: Guy Sternberg (*Quercus agrifolia*). Photos in Fig. 5: (a) J. Linsdale; (b) J. Dickinson.

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