

8. External Impacts on Internal Dynamics: Effects of Paleoclimatic and Demographic Variability on Acorn Exploitation along the Central California Coast

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Abstract. Research into human-environment interaction in California prehistory often focuses on either the internal dynamics of adaptive decisions or the external impacts of environmental change. While both processes were surely driving prehistoric variability, integrating these approaches is not altogether straightforward. Here we outline an inclusive approach examining the exploitation of acorn habitats in Central California. Acorns were critically important to many ethnographic groups in Native California, but the intensive use of acorns appears to be a Late Holocene phenomenon. Most research approaches the increased reliance on acorns as a process governed by internal dynamics linked to demographically-driven resource intensification, but there are strong reasons to believe that climatic variability also structured acorn use. Here we link internal and external human-environmental dynamics through a formal behavioral ecological model. This model provides clear predictions that can be used to identify departures from expected internal dynamics linked to external factors driven by paleoenvironmental change. Results show that prehistoric occupation along the central California coast shifts into interior oak-dominated regions with increasing population densities, consistent with model expectations of internally-driven resource intensification. However, acorn use is also affected by climate: foragers are less likely to live in productive acorn habitats during periods of drought. These findings show that neither internal nor external patterns can completely account for variability in prehistoric decisions, but that integrating these through formal ecological models can provide insights into the external impacts on internal dynamics that structure broad patterns in prehistory.

Introduction

Research into California prehistory often focuses on either the internal dynamics of adaptive decisions (e.g., Basgall 1987; Hildebrandt and Jones 1992) or the external impacts of environmental change (e.g., Jones et al. 1999; Kennett et al. 2007). While both processes surely

drove variability in prehistory, integrating internal and external dynamics is not a straightforward endeavor. Here we outline an inclusive approach using spatially explicit predictions from a behavioral ecological model to explain variability in the exploitation of acorn habitats along the central California coast.

Acorns were critically important to many ethnographic groups in Native California (Gifford 1936), but the intensive use of acorns appears to be a late Holocene phenomenon. Most research approaches the increased reliance on acorns as a process governed by internal (endogenous) dynamics linked to demographically-driven resource intensification (Basgall 1987; Coddling et al. 2012). Because acorns offer a low rate of nutrient return relative to the time required to process and store them (Simms 1985, Wohlgemuth 2010, also Morgan 2012), model-based predictions from behavioral ecology (e.g., MacArthur and Pianka 1966, Morgan 2015) suggest that foragers should only begin relying on such a low profitability resource when more profitable foods decline in abundance due to processes such as resource depression (e.g., Broughton 1994).

There are strong reasons to suspect that external (exogenous) factors such as climatic variability also mediated acorn use. Ecological research has shown that acorn productivity in central California (Koenig et al. 1996) and elsewhere (Sánchez-Humanes and Espelta 2011) decreases significantly with prolonged drought. As such, reduced rainfall should not only depress the terrestrial environment overall, but could have had a particularly disruptive effect on foragers reliant on acorns as a staple food source. Indeed, periods of drought should have a differential impact on foragers depending on their subsistence strategies: those reliant on resources that are insensitive to drought, like marine foods, should be relatively resilient; while those reliant on resources that are particularly sensitive to drought, like acorns, should be dramatically impacted.

To examine these interactions, here we link internal and external human-environmental dynamics through a formal model from behavioral and population ecology. Known as the Ideal Free Distribution (IFD) model (Fretwell and Lucas 1969), recent applications have provided insights into the factors structuring land-use patterns in prehistoric California (e.g., Coddling and Jones 2013; Coddling et al. 2012; Jazwa et al. 2013; Kennett 2005; Kennett et al. 2009; Winterhalder et al. 2010) and elsewhere (e.g., Allen and O'Connell 2008; Kennett and Winterhalder 2009). The IFD establishes clear settlement predictions based on the dynamic interactions between demography and habitat suitability. Specifically, the model predicts that individuals should choose to occupy the most suitable habitats available until a point at which demographic pressure (anthropogenic resource depression, competition with conspecifics, etc.) in those habitats causes individuals to do better by moving into less suitable and less densely occupied patches. Thus, holding climatic change constant, long-term increases in population densities should cause foragers to cascade into lower and lower suitability patches.

The greatest difficulty in applying the IFD archaeologically is that suitability must be explicitly operationalized in each case, ideally using some proxy for resource acquisition efficiency that adequately captures how an individual would be expected to evaluate the profitability of alternative habitats. To do this, we rely on logic from prey and patch choice models (MacArthur and Pianka 1966). We begin by defining habitats as aggregations of

patches and patches as aggregations of resources. Resources vary in their profitability (e.g., Simms 1985) and patch profitability should vary based on the abundance of the highest profitability resources within the patch. Habitats should then vary in suitability based on the abundance of high profitability patches. Along the central coast of California, high profitability marine resources (e.g., fish, marine vertebrates) are only available directly on the littoral and high profitability terrestrial resources should be more abundant along the coast than in the interior as a result of differences in precipitation. As such, habitats on the coastal plain with littoral patches of abundant marine resources and mixed chaparral/grassland patches with abundant terrestrial resources should be more suitable than inland habitats dominated by oak patches. While inland oak habitats are not necessarily resource poor, high profitability resources should occur in lower densities in the interior, with the most abundant food resource—acorns—offering lower net yields per time spent handling compared with resources found along the coast. As such, these inland habitats should be of lower overall suitability when compared with the coast, but provide abundant, low profitability resources that populations can exploit when the more profitable alternative are less available.

Predictions

Linking these estimates of habitat suitability with basic IFD model dynamics, we predict that foragers should have prioritized settlement along productive coastal habitats (see also Coddling et al. 2012; Jones 1991), only moving into interior oak patches once demographic pressure reduced per capita gains in high suitability coastal patches. However, this simple prediction may be confounded by climatic variability. If climatically-induced reductions in environmental productivity differentially affect oak habitats relative to neighboring coastal habitats, then prolonged droughts may decrease the overall suitability of inland habitats to a point where foragers could achieve higher per capita gains even in densely occupied coastal habitats, resulting in a shift in populations out of inland habitats and into coastal ones, regardless of existing demographic pressure. Approaching the problem in this way allows for the identification of departures from expected internal dynamics linked to external factors driven by paleoenvironmental change. After discussing the data and methods used in this paper, we test these predictions, examining impact of internal and external factors on individual's decisions to settle in acorn habitats.

Methods and data

Examining the interaction between demographic and climatic variability on habitat choice requires a combination of internal (endogenous) and external (exogenous) variables. For this study, these include proxies of human population, habitat choice, and climate.

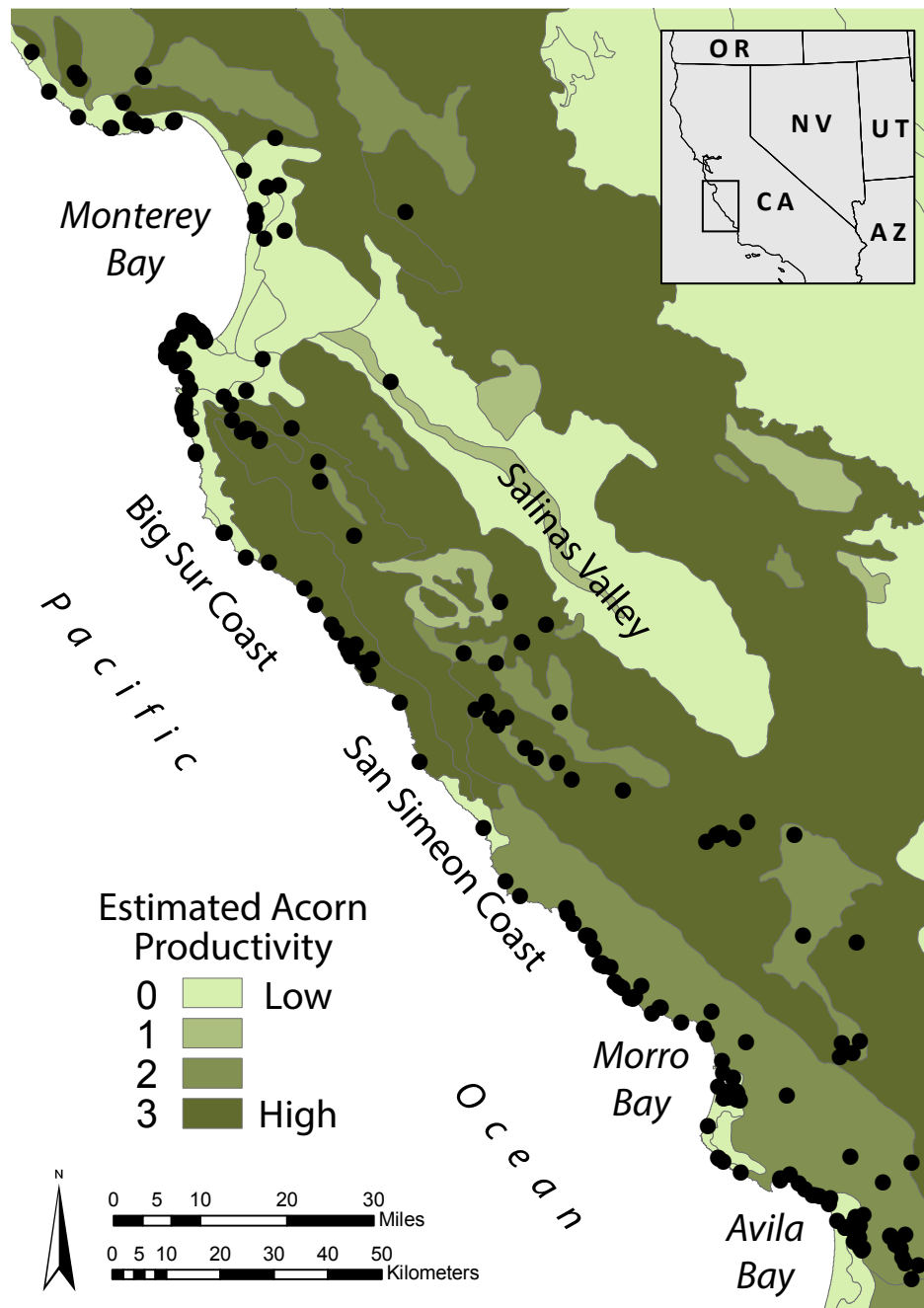


Figure 8.1. Radiocarbon-dated archaeological sites along the Central Coast of California relative to estimated historic acorn productivity (Wohlgemuth 2010).

As a proxy for population densities, we use a database of radiocarbon-dated components in Santa Cruz, Monterey and San Luis Obispo Counties (Jones et al. 2007). Occupational histories for each site are determined using all the calibrated radiocarbon dates available summed across the Holocene record in 100 year intervals (Jones et al. 2007; Coddling et al. 2012). A single Paleoindian component marked by a fluted point is undated, but is included

here at 12kya. One-hundred year bins were chosen as the minimum meaningful unit given the measurement error and calibration uncertainty inherent in radiocarbon dates; the former is a particular problem with legacy data like that incorporated into regional databases. A site was considered occupied for any given 100-year interval if that interval overlapped with the 95% confidence interval reading of a calibrated radiocarbon date. This broadens the number of bins considered occupied for a given radiocarbon date, but may be more archaeologically meaningful than a summed radiocarbon probability distribution as it incorporates periods of time when the site was likely occupied but for which a probability distribution around a central tendency reading would not necessarily indicate as such. This method generally provides results consistent with other methods used to estimate prehistoric populations (Williams 2012). In this way, each interval is treated as an archaeological component (sensu Phillips and Willey 1953). To account for preservation bias that renders older components less common, we apply a taphonomic correction following Surovell et al. (2009), here set at a maximum of 100 sites per period. By empirically modeling the difference between observed volcanic events in sedimentary contexts with those in atmospheric contexts from the Greenland Ice Core record, this approach allows for a standard correction factor to be applied in order to estimate the number of actual sites from the number of observed sites. Both observed and corrected population estimates are used in quantitative models to determine the effect of demography on acorn habitat use. While a useful control on potential taphonomic bias, this approach is certainly not without its problems. This method produces a global correction assuming the equal loss of sites across all landforms, but taphonomic loss may result from specific depositional or erosional events that affect some locations and not others (e.g., sea level rise), which can only be corrected through local geomorphological research (Ballenger and Marby 2011). Unfortunately, the work necessary to perform this analysis has not been undertaken in the study area. While taphonomy thus remains a confounding factor, and we do not account for sample size effects, our qualitative interpretations only treat high-magnitude and long-duration shifts as meaningful (see Contreras and Meadows 2014). Further research addressing taphonomy, geomorphology and sampling, may improve the resolution of demographic patterns.

From these data, we also approximate habitat choice through time by linking the spatial location of occupied components to landscape estimates of acorn productivity (Figure 8.1). Historic potential climax vegetation from Küchler (1977) was evaluated by Wohlge-muth (2010) to rank habitats by acorn nut productivity. While the spatial distribution of these habitats surely changed at least modestly throughout the Holocene, the relative values between patches should remain stable through the record. Because oaks of the same species should respond similarly to climatic variability, reductions in regional productivity should reduce the relative ranking of each oak habitat equally so that high ranking areas remain high relative to low ranking areas. Major ecotonal shifts in prehistory may invalidate this assumption, but the fine-grained paleoecological data to account for these shifts are currently unavailable. We extract vegetation data for each dated component using ArcMap (ESRI 2010). The total number of sites in highly productive acorn habitats (rank 3, see Figure 8.1) is divided by the total number of sites occupied for each 100 year interval. This results in an estimate of the proportion of sites located in highly productive nut habitats in 100 year

slices across the Holocene record. As a proxy for the reliance on acorns, this is the main dependent variable used in analysis.

Two climatic proxies are used to examine the external impacts on acorn habitat settlement. First, we rely on Cook and colleague's (1999, 2004) gridded reconstructions of drought severity. Based on tree-ring reconstructions, these data provide spatially-explicit estimates of drought severity normalized as the Palmer Drought Severity Index (PDSI). PDSI represents the amount of soil moisture available relative to the long-term average such that low values indicate dry conditions. The second proxy is an estimate of local sea surface temperatures from a marine core taken off the Santa Barbara coast (south of the study area; Kennett and Kennett 2000). Sea surface temperatures (SST) are approximated using oxygen isotope values from surface dwelling foraminifera (*G. bulloides*; Kennett and Kennett 2000; Kennett et al. 2007). Values are reported as the ratio of O^{16} and O^{18} relative to a standard (δO^{18} PDB ‰). To make it comparable with the demographic and settlement data, SST data is averaged across 100 year intervals using the `wapply` function in the `gplots` library (Warnes et al. 2014) in R (R Development Core Team 2014). In order to examine how these two climatic proxies vary with one another over the last 2000 years, we smooth both trends using the `loess.as` function from the `fANCOVA` package (Wang 2010) in R (R Development Core Team 2014). Smoothing terms were established using a generalized covariance function with a first order polynomial (Figure 8.2, thick black lines). For visualization purposes, PDSI data are also shown in Figure 8.2 smoothed with a second order degree polynomial.

In order to model the effect of each independent variable (demographic and climatic proxies) on the dependent variable (the proportion of sites located in high productivity acorn habitats), we rely on generalized additive models (GAM). GAMs break up independent (predictor) variables into a series of parametric fits with non-parametric smooth terms (splines) tied together at a series of 'knots' (Hastie and Tibshirani, 1990; Wood, 2012). GAMs trade-off between maximizing goodness of fit (minimizing residual deviance) and maximizing parsimony (minimizing the degrees of freedom, df). We take a conservative approach by minimizing the number of knots used in each model in order to maximize parsimony. GAMs can examine the response of a dependent variable to an independent variable while holding the effects of additional independent variables constant. We do this below to examine the combined effects of demographic and climatic factors on the proportion of sites located within productive oak habitats. Since the primary dependent variable is a proportion that is constrained to vary between zero and one, all models assume a binomial distribution with a logit link using a quasi-likelihood estimation (unless otherwise noted). Results report the number of knots (k) used in the model, the log-likelihood r-square (R_L^2) which measures the proportion of deviance explained by the independent variable(s), the F statistic of the independent variable, and the p -value. To illustrate the model results, we present (Fig. 8.3) partial residual plots that show the effect of independent variable on the response variable while holding any effect of additional independent variables constant. These approach allows us to determine how populations (the number of occupied sites) and climate (SST) influence the degree to which local populations relied on acorns (the proportion of sites located in highly productive acorn habitats).

Methodological Vignette: Spatially Explicit Behavioral Ecology (SEBE)

Spatially explicit behavioral ecology links methods and models from GIS and spatial analysis to test theoretical predictions derived from behavioral ecology. The approach provides three specific advantages to help answer questions about human-environmental dynamics. First, because the BE approach reduces complex problems to their constituent parts, researchers are forced to articulate key components to be analyzed. This helps frame the question and directs research towards the specific data needed to answer the question. Second, by generating predictions from a general theory of behavior, researchers are able to nominate causal relationships a priori (Bird and O'Connell 2006, Coddling and Bird 2015, O'Connell 1995), which helps to reduce spurious correlations. Finally, spatially explicit models provide an opportunity to link human behavior to specific environmental conditions. This can be analytically trying as it adds a spatial dimension to archaeological time-series analyses, but the process allows researchers to link specific aspects of ecological variability to human decisions across space and through time.

Applying this approach requires that researchers first link a research problem to an appropriate foraging model (or vice versa) depending on the scope and scale of the question of interest (for a recent review, see Coddling and Bird 2015). Model variables will help researchers identify the data necessary to answer the question, which will frequently include spatially-explicit time-series data that tie material proxies of human decisions (e.g., faunal remains or settlement chronologies) to paleoenvironmental data (e.g., estimates of resource abundance or environmental productivity). Key here is the compilation of data on comparable time-spaces scales that can be used to identify how humans adapt to and modify their surrounding environments.

To date, this work has been most useful in explaining hunter-gatherer foraging ecology and behavior. Examples include modeling spatial variability in men's and women's foraging returns (Zeanah 2004), hunter-gatherer foraging radii (Morgan 2008), and habitat use in response to climate change (Morgan 2009). Growing applications examine patterns of colonization across novel landscapes (e.g., Allen and O'Connell 2008, Kennett 2005, O'Connell and Allen 2012), with implications for understanding the origins of ethnic diversity (Coddling and Jones 2013) and the emergence of social inequality (e.g., Winterhalder et al. 2010).

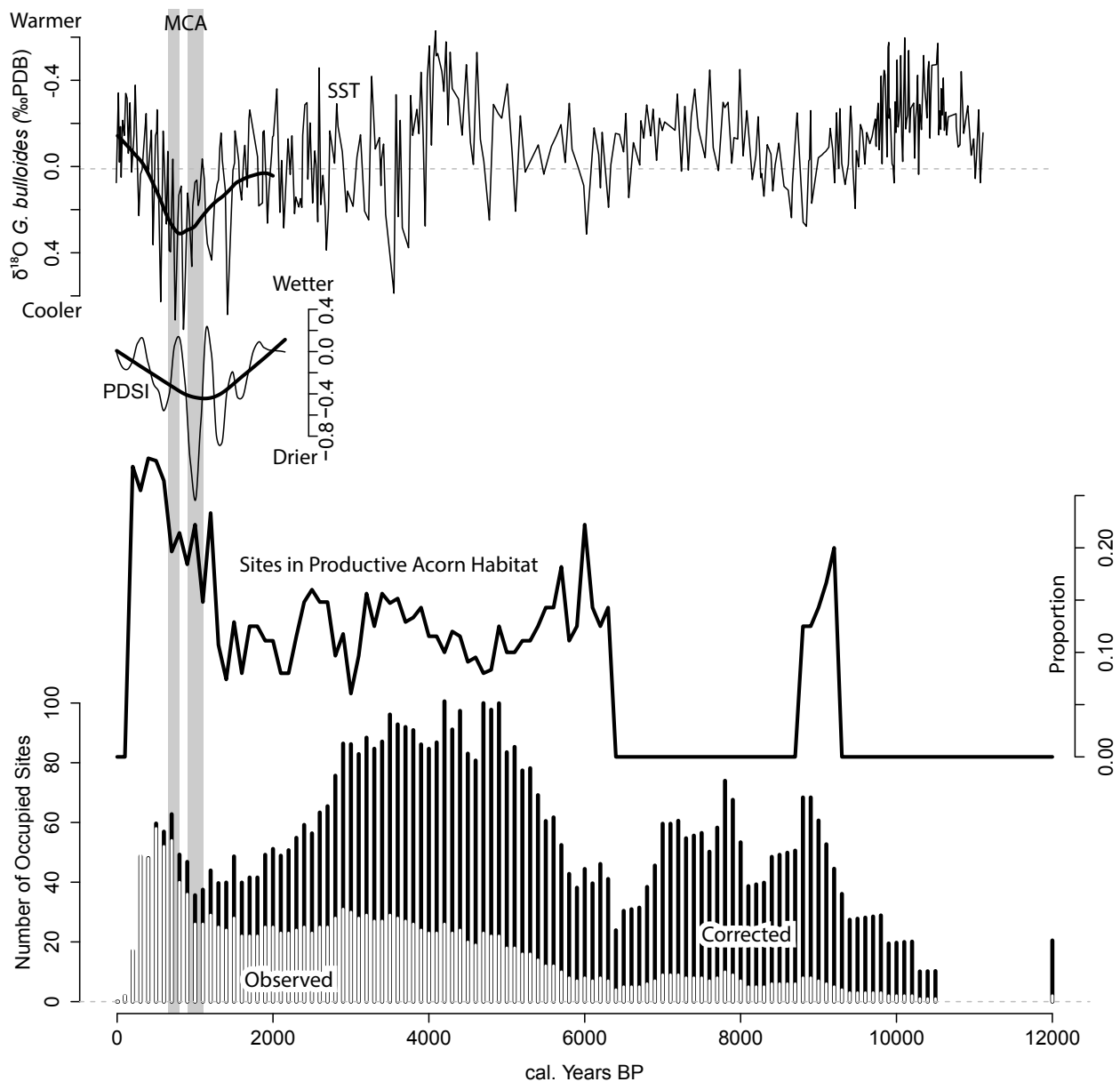


Figure 8.2. Summary of demographic, settlement and climatic proxies for the study area across the Holocene. Population proxies include observed and taphonomically corrected occupational histories at 100 year intervals. Settlement data reports the proportion of those sites located within productive acorn habitats. Climatic data includes smoothed values of local Palmer Drought Severity Index (PDSI) from Cook et al. (1999, 2004) and inferred sea surface temperatures (SST) from Kennett and colleagues (1995, 2007, Kennett and Kennett 2000). Droughts associated with the Medieval Climatic Anomaly (MCA) are shown in grey (Stine 1994).

Results

Internal Dynamics: does demographic pressure drive acorn exploitation?

An examination of the observed occupational sequence shows that populations increase linearly through the Holocene (Figure 8.2). When corrected for taphonomic bias, populations still fluctuate throughout the sequence, but the trend is nonlinear. As shown in Figure 8.2, there are several periods of high population: one from about 10,000 to 7,000 years ago, a second from about 6,000 to 2,500 years ago, and a third beginning about 1000 years ago.

These fluctuations in populations structured decisions to settle in highly productive acorn habitats. Throughout the Holocene, the proportion of sites located in highly productive acorn habitats increases significantly as a function of the total number of sites occupied ($k = 3, R_L^2 = 0.43, F = 35.21, p < 0.0001$). This trend is also manifested in the taphonomically corrected estimates of population density ($k = 3, R_L^2 = 0.16, F = 6.99, p = 0.0015$) although the proportion of the deviance explained is greatly reduced from 43% to 16%. These results confirm the prediction that individuals only move into acorn producing habitats when population densities are high.

External Impacts: do drier climates limit acorn exploitation?

Over the last 2000 years, drought severity worsened significantly when sea surface temperatures cooled along the central coast of California (Gaussian GAM, $k = 3, R_L^2 = 0.73, F = 2805, p < 0.0001$; see Figure 8.2). While sea surface temperatures in the region do not correspond perfectly with terrestrial productivity, this empirical relationship confirms previous findings that SST may be a reliable proxy for variability in local terrestrial climate (see Kennett and Kennett 2000, Kennett et al. 2007, Jones and Kennett 1999).

Using SST to examine the effect of climate on acorn habitat use across the entire Holocene record shows that the proportion of sites in productive oak habitats declines significantly with decreasing sea surface temperature ($k = 3, R_L^2 = 0.23, F = 12.79, p < 0.0001$). Because cooler sea surface temperatures are associated with decreased terrestrial productivity, this finding suggests that drier climates limit acorn exploitation.

External Impacts on Internal Dynamics: what are the combined effects of demography and climate?

To examine the linked effect of demographic and climatic factors, we combine these data in a single model that controls for the interaction of both predictor variables. This model shows that both demography and climate have a significant effect on decisions to move into oak habitats (Figure 8.3, $k = 3, R_L^2 = 0.46, p < 0.0001$), with demography ($F = 19.15$) having a greater impact than climate ($F = 6.03$). These trends hold even with the taphonomically corrected site data ($k = 3, R_L^2 = 0.38, p < 0.0001$), but with climate ($F = 33.92$) having a greater effect than demography ($F = 9.15$). The results indicate that holding climate constant, demographic pressure remains a significant factor in determining settlement choice (Figure 8.3, left). Likewise, holding population constant, climate has a significant effect on settlement decisions (Figure 8.3, right). These trends and some remaining anomalies are discussed below.

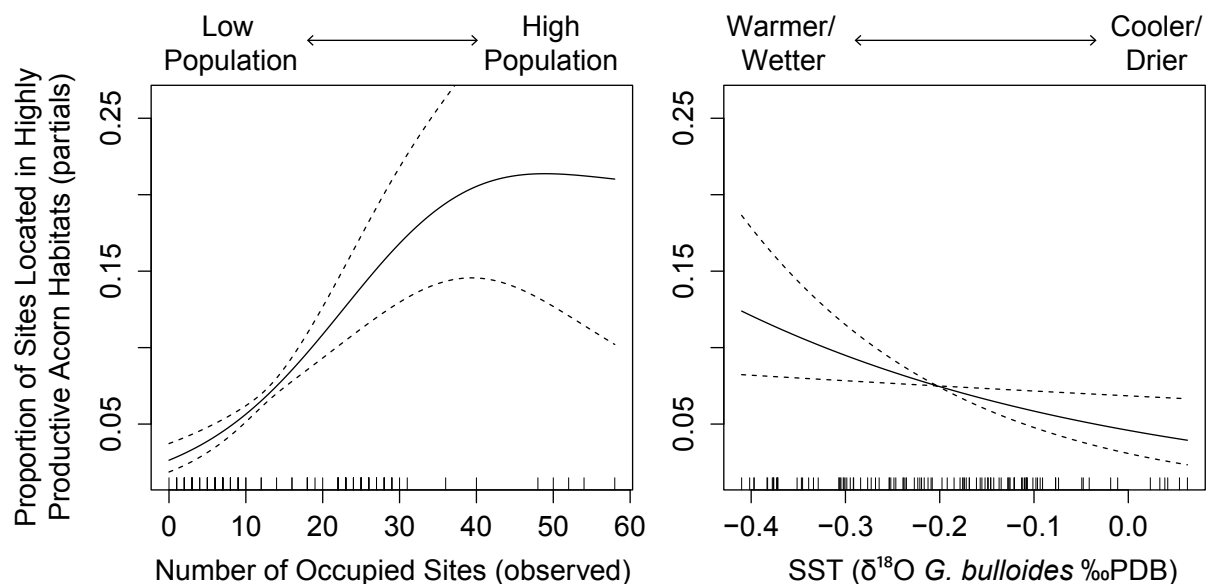


Figure 8.3. Partial residual plots of generalized additive model results showing the combined effect of observed population (left) and sea surface temperature (right) on the proportion of sites located in productive acorn habitats. These results show that as populations increase, people move into productive acorn habitats (left); but when conditions are drier, fewer people settle in productive acorn habitats (right). Data correspond to time series trends shown in Figure 8.2 sampled at 100-year intervals. These plots show the relationship between the response variable (proportion of sites) and each independent variable (number of occupied sites and sea surface temperature) holding the effect of the other independent variable constant (e.g., the effect of SST on the proportion of sites in acorn habitats while holding the effect of the number of sites constant).

Discussion

The results of this study highlight the importance of an approach that combines the effects of external and internal factors on prehistoric human decisions. Overall, the results show that both demographic and climatic factors structured settlement in productive acorn habitats through the Holocene. As predicted by the IFD, individuals chose to move into these relatively low profitability habitats as a result of demographic pressure. But, this decision was also mediated by climate: individuals were less likely to settle in oak habitats during times of decreased overall environmental productivity.

At particular points in the regional prehistory, either demography or climate appears to have been more dominant. Between about 10,000 and 6000 years ago, individuals rarely settled in oak habitats. While climatic proxies suggest that terrestrial environment was relatively productive during this time, foragers chose not to exploit acorns due to limited demographic competition in higher suitability patches. This is supported by faunal evidence

suggesting that foragers experienced relatively high returns with more profitable resources during this time (Jones et al. 2008a, 2009).

At later points, these two factors seem to have worked in concert. Beginning approximately 6000 years ago, forager populations expanded while climate was ameliorating. This resulted in the first large-scale population expansion into productive oak habitats. This is also the same time period when the proportion of acorn-specific processing equipment (mortars and pestles) increased above 50% of groundstone assemblages in the region (Coddling et al. 2012; also see Stevens and McElreath 2015). Without climatic impediments, demographic pressure pushed foragers into exploiting acorns intensively for the first time.

These trends decouple beginning about 3000 years ago, when forager populations either plateaued (observed site counts) or began to decline (corrected site counts). In this context, the proportion of sites in highly productive oak habitats remained relatively stable, despite increasing aridity. Indeed, despite radical changes in other subsistence patterns during this interval (e.g., Coddling and Jones 2007, Coddling et al. 2010, Jones et al. 1999, 2007) acorn habitat use remained relatively important even through the two mega-droughts associated with the Medieval Climatic Anomaly (MCA; ca. 1100-900 and 800-650 years ago; Stine 1994). Contrary to our predictions at the outset, this may result from these extreme droughts dampening all terrestrial environments equally so that relative habitat rank remained the same. But given the response of oaks to drought, this seems unlikely. Alternatively, it could be that acorns remained important due to their storability. If the MCA increased subsistence uncertainty, foragers may have responded by maintaining fall habitation sites in highly productive oak patches where they could potentially acquire enough acorns in order to reduce subsistence variance later in the year. Finer-grained data addressing seasonality of occupation would be needed to evaluate possibilities like this one.

At the end of the MCA, the dampening effects of drought on habitat suitability were removed. Populations begin to increase during this time of climatic amelioration coincident with a dramatic increase in the proportion of sites located in oak habitats, reaching the highest point in prehistory. These late prehistoric shifts in settlement mark the onset of intensive acorn use recorded ethnographically. These patterns are likely dominated by seasonal resource extractions camps occupied in the fall (Jones et al. 2008b). Perhaps the most notable implication of this trend is that the increased use of acorn habitats exceeds what would be predicted either by demographic or climatic trends. Considering the corrected site counts, previous periods in prehistory saw greater increases in populations and the climatic records indicate higher levels of terrestrial productivity.

There are perhaps two possible explanations for this late prehistoric anomaly that center on additional constraints associated with the shift to an acorn-based economy. First, ethnographic and ecological evidence suggests that the reliable exploitation of acorns may require the frequent application of fire in order to make oak groves reliable and productive (Anderson 2005, Anderson and Rosenthal 2015, Lightfoot et al. 2013). If this is true, then the increase in oak habitat exploitation late in the record may mark the onset of anthropogenic fire regimes recorded ethnographically. The second potential explanation involves constraints on the shift from immediate to delayed return economies (Woodburn 1982). Because the intensive use of acorns requires that crops be gathered and stored, this economic

shift requires paired shifts in social institutions associated with the management of private property (Bettinger 2015, Bowles and Choi 2013). It is possible that the development of social institutions designed to deal with the collective action problems associated with stored food did not emerge until late in the prehistoric record.

Conclusion

This paper examines the external impacts of climatic variability and the internal dynamics of demography on forager settlement and subsistence. The results illustrate how incorporating both factors into analysis may be necessary to explain prehistoric decisions. By linking these factors within a formal ecological model, this approach limits the probability of spurious correlations by specifying causal predictions a priori. While this example illustrates the usefulness of this approach in a regional context focused on acorn use, it has the potential to be a productive framework in explaining broader and more varied patterns across other ecological, subsistence and social settings.

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