

Phytolith evidence for the extent and nature of prehistoric Californian grasslands

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Abstract

Californian grasslands have been radically transformed by cultivation and exotic species invasions that began with European settlement in 1769. Because native species contribute only a small percentage of total vegetation cover at most grassland sites in California today, there has been a long-standing controversy regarding the extent and composition of prehistoric grasslands. We used phytolith analysis of soil samples from 153 spatially diverse grassland sites currently cultivated or dominated by exotic annual grasses to provide the first direct evidence that, except for areas near the coast, grass was generally a minor component of the vegetation. Most of the arid, non-wetland Central Valley and surrounding foothills probably had very low grass cover. Combining our data with historical accounts of vegetation encountered by early explorers in California and relict analysis of native species in existing grassland patches, it appears that while the extent of prehistoric grassland was probably similar to the current extent of exotic annual grassland, most areas were likely dominated by a highly diverse assemblage of herbaceous species, composed largely of annual forbs adapted to exploit local environmental heterogeneity. Phytolith analysis should be routinely performed in California to guide grassland restoration efforts. The technique can also be used to reconstruct prehistoric vegetation of highly altered grassland ecosystems worldwide.

Keywords

bunchgrass, coastal prairie, forbs, palaeoecology, reference conditions, restoration, valley grassland

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Introduction

Grassland, defined as land on which the vegetation is dominated by grasses, grass-like plants and/or forbs (Natural Resources Conservation Service (NRCS), 1997), currently covers ~10% of California's land area, including >5,000,000 ha classified valley grassland, ~4,000,000 ha in oak savanna understory and >350,000 ha classified coastal prairie (Bartolome et al., 2007; Ford and Hayes, 2007). These grassland types in California are loosely termed California annual grassland (CAG) because they are currently dominated by suites of exotic annual grasses and forbs that invaded following European settlement beginning in 1769 (Heady, 1977).

Because the radical transformation of the 19th-century grassland landscape by cultivation and exotic plant invasion was so rapid and eyewitness accounts of prior vegetation were not produced by trained botanists, the extent and nature of prehistoric grasslands have been the subject of considerable speculation based on circumstantial evidence for nearly a century. Grassland extent was assumed to include the area currently covered by CAG, as well as most of the currently cultivated Central Valley (Kuchler, 1977). Whether grass species dominated prehistoric Californian grasslands is unknown (Jackson and Bartolome, 2007). An early hypothesis regarding species composition, based on observations of disturbed relict patches and largely unquestioned for several decades, stated that prehistoric grassland cover was dominated by native bunchgrasses, particularly *Stipa pulchra* (Clements, 1934; Heady, 1977, 1988). Recent interpretations of historical accounts (Minnich, 2008) and analysis of relatively undisturbed relict grassland patches (Holstein, 2001; Schiffman, 2007) have challenged this paradigm, postulating that many areas of CAG were dominated by native forbs rather than bunchgrasses

and *Stipa pulchra* was not dominant in the Central Valley. Recent work on small-scale spatial patterns has shown that local soil chemistry plays an important role in determining native species dominance in coast range grasslands and coastal prairie, suggesting a high degree of small-scale heterogeneity in prehistoric grassland species composition (Bartolome et al., 2008; Gea-Izquierdo et al., 2007).

Phytolith analysis is a palaeoecological technique particularly well suited for testing hypotheses concerning prehistoric grasslands. Phytoliths are microscopic, weathering-resistant particles of silica formed in certain plant taxa that are released from decomposing litter and accumulate over time in the soil, eventually contributing 0.1–3% to the soil dry weight (Drees et al., 1989). Grasses are prolific phytolith producers (1–15% dry weight; Epstein, 1999) compared to most taxa; grass phytoliths remain in the soil for several hundred to thousands of years in most environments (Piperno, 2006). The presence of >1% dry weight phytoliths in the soil, when composed largely of distinctive grass morphotypes (particularly short cells, specialized silica accumulating cells found only in grasses, as opposed to elongate and appendage morphotypes, which are found not only in grasses but also in many other plant families), has been used extensively as an indicator of long-term

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grass-dominated vegetation at North American sites (summarized in Evett et al., 2006). Studies at several sites in California have successfully used soil phytolith content to determine grass dominance (Bicknell et al., 1993; Evett et al., 2006, 2007, 2012; Hopkinson and Huntsinger, 2005). Additionally, even though they are C₃ grasses (typical of almost all native and exotic grasses commonly found in California), the postulated dominant bunchgrass in prehistoric valley grassland, *Stipa pulchra*, and an important coastal prairie native bunchgrass, *Danthonia californica*, produce bilobate phytoliths, a short cell morphotype not produced by any common exotic grass species, which produce only rondel and crenate short cells. Soil phytolith assemblages with high proportions of bilobate phytoliths indicate that *Stipa* and/or *Danthonia* were likely long-term dominant (Evett et al., 2012). An early phytolith study in California used this fact to show that a site in the Sacramento Valley currently dominated by exotic annual grasses was probably prehistorically dominated by *Stipa pulchra* (Bartolome et al., 1986).

Soil phytolith content can be used to estimate the degree of grass dominance at Californian sites because phytolith extractions from reference material have shown that other than grasses, very few plant species commonly found in grasslands in California, native or exotic, produce abundant biogenic silica (Evett et al., 2006; Evett, unpublished data). Studying a mosaic of CAG, shrub and forested sites in northern California, Evett et al. (2012) proposed distinguishing sites with substantial long-term grass cover from other sites by using a $\geq 0.3\%$ soil phytolith weight threshold combined with grass phytolith morphotype abundance parameters.

In this study, we use phytolith analysis to calculate soil phytolith parameters for 153 near-surface soil samples from sites currently dominated by CAG throughout California to identify regions with substantial prehistoric grass cover. We then combine these data with published historical and observational data to describe the likely extent and nature of California's prehistoric grasslands.

Methods

Soil samples were obtained from a soil archive (maintained by Ron Amundson at the University of California, Berkeley) of >2000 soil profiles collected statewide during the 1920s–1970s (Baisden et al., 2002). Each archive sample is labelled with soil series, horizon depth designation, county of origin and exact location information when available. A profile was included in the sampling universe if the NRCS soil series description (<http://soils.usda.gov/technical/classification/osd/index.html>) indicated CAG is (or would be, if currently cultivated) typically the dominant vegetation on this series. Sample selection was not random because many profiles were spatially clumped; an effort was made to include samples from as many counties as possible. Also, because we wanted to include samples from soil series representative of the largest possible spatial area within the state's postulated prehistoric grassland regions (Kuchler, 1977) and because sites classified within the same soil series are assumed more likely to have similar vegetation histories, preference was given to profiles from soil series covering the most area. When available, two or more profiles were sampled from soil series covering >40,000 ha to improve accuracy and examine phytolith assemblage homogeneity within a series. Several profiles included in the study that satisfied these criteria had no location information beyond county. Profiles with site location information were checked using Google Earth with a soil series overlay (Beaudette and O'Geen, 2009) to ensure location and series name accuracy. A few series names have changed since the soil profiles were collected; current series names were assigned to each located site.

NRCS descriptions of soil profile horizon depth, texture and colour were compared with archive profile samples to ensure archive soils were accurately labelled.

A total of 5 g of soil from the uppermost A-horizon in the profile (and also the horizon immediately below this horizon) was collected for each selected archive site and dried for 8 h at 60°C. Phytoliths were extracted using a modified closed vessel microwave acid digestion procedure to remove carbonates and oxidize organic matter (Parr, 2002), followed by sieving to remove particles >100 μ , heavy liquid flotation in zinc bromide (specific gravity 2.30) to separate biogenic from mineral silica, and timed gravity sedimentation to remove clays (Piperno, 2006). After being dried and weighed, the phytolith extract was suspended in a measured quantity of immersion oil. A drop of the suspension was mounted on a glass slide and viewed at 400 \times magnification under a microscope. Soil phytolith dry weight was estimated by scanning 10 randomly chosen microscope fields on a single slide, using an eyepiece grid to estimate the proportional weight of non-phytolith material (e.g. diatoms, mineral particles, charcoal, sponge spicules), and subtracting this from total extract dry weight. Absolute counts of phytolith morphotypes (number of phytoliths/gram of soil) were obtained by scanning slides in non-overlapping transects and recording the number of microscope fields required to tally at least 200 identifiable phytolith morphotypes (Albert et al., 1999; Evett et al., 2012). All phytoliths were manually rotated to view all aspects to ensure positive identification of morphotypes.

Results

We sampled soils from 153 archive sites located in 29 counties, including 120 soil series encompassing $\sim 5,000,000$ ha, representing >50% of California's total grassland area (supplementary Table 1, available online). Site spatial distribution within postulated prehistoric grassland areas, while partially clumped with several blank regions not sampled, covered most of the latitudinal and longitudinal range (Figure 1).

We found very low soil phytolith content, <0.10% at 60% of the sites (Figure 2). Only 26 sites (17%) had soil phytolith content $\geq 0.30\%$, the arbitrary threshold previously used to indicate substantial long-term grass cover, although not necessarily grass-dominated vegetation (Evett et al., 2012). Phytolith content of subsurface soil samples was less than content in the uppermost A-horizon samples at all sites; these samples were not analysed further.

Grass short cell morphotypes contributed substantially to the phytolith assemblage at most sites (supplementary Table 1). Counts of grass phytolith morphotypes at each site generally mirrored the total phytolith percent weight data. For example, after removing two obvious outliers, total short cells was strongly correlated with percent weight ($R^2 = 0.89$; Figure 3). Bilobate phytoliths, indicating the presence of *Stipa* and/or *Danthonia* species, were found at 73 sites, but concentration >20,000 bilobates/g soil with bilobate/total phytolith ratio above 0.10 (shown by asterisks in supplementary Table 1, available online), likely indicating substantial prehistoric cover of these native species, was found at only 10 sites, all within 50 km of the coast.

While grass phytolith parameters for the 32 soil series sampled at more than one site suggest possible homogeneity within a series, many more sites would be required to reach statistical significance: 24 series showed little difference between sites, 5 showed minor differences, and 3 pairs clearly showed one of the sites was grass-dominated, the other not (supplementary Table 1, available online).

There were two spatial distribution patterns evident for grass-dominated sites (Figure 1): (1) no grass-dominated sites were

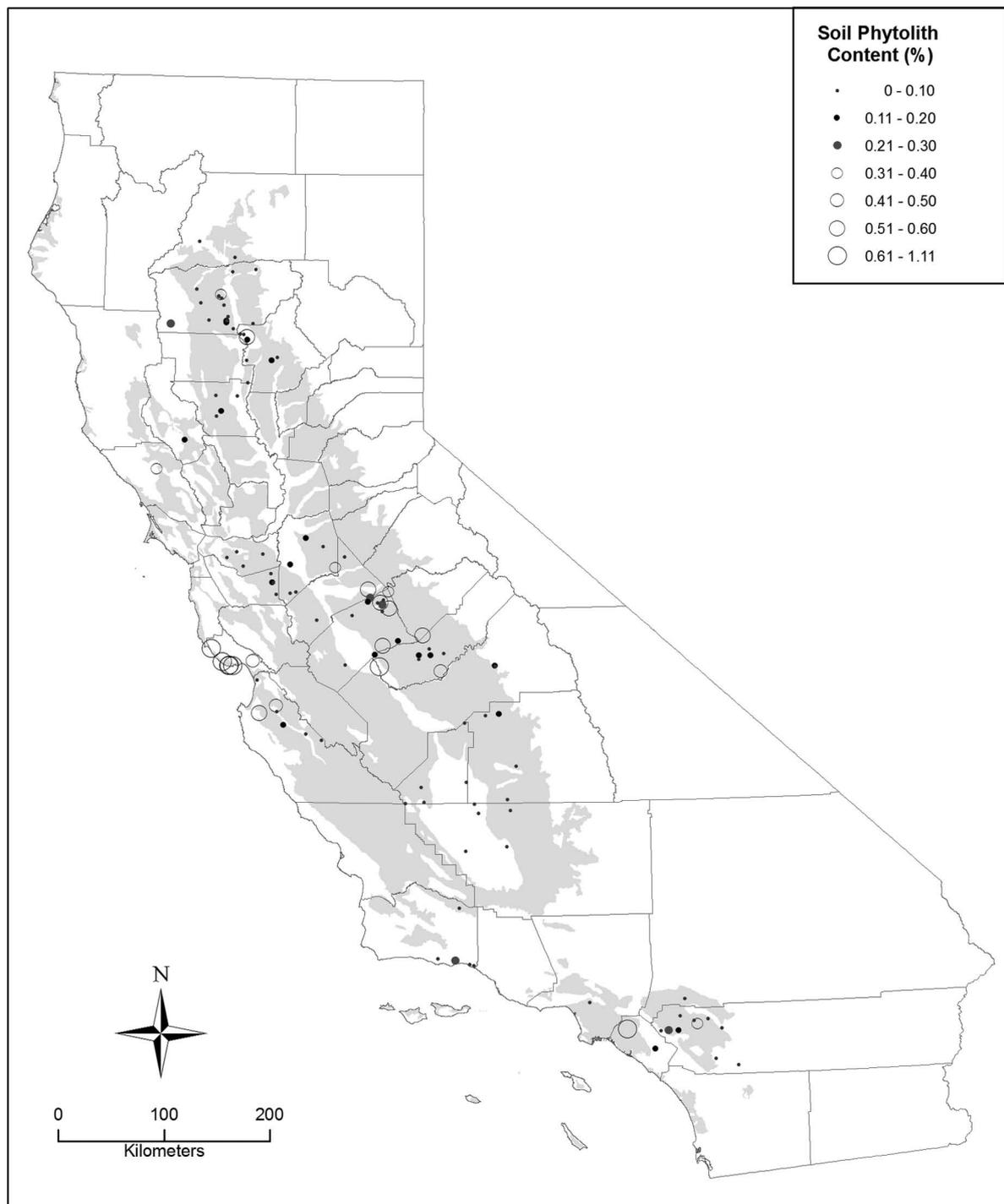


Figure 1. Soil phytolith content classes for sampled sites that have location data. Lines are county boundaries; shaded area delineates regions in California with vegetation types previously thought to have substantial prehistoric grass cover (Kuchler, 1977). Open circles represent sites above the 0.30% soil phytolith content threshold that indicates substantial prehistoric grass cover; closed circles represent sites below the threshold.

found in the Central Valley south of the San Joaquin River and (2) sites located near the coast were more likely grass-dominated than inland sites.

Discussion

The phytolith evidence strongly indicates that most regions in California currently dominated by exotic annual grasses were not dominated by native grasses prior to European settlement; in fact, many of these regions probably had very low grass cover. In particular, contrary to the assertion of Clements (1934), most of the

Central Valley was unlikely to have supported a bunchgrass prairie dominated by *Stipa pulchra*.

Our results provide the first direct evidence supporting an emerging hypothesis that most Californian prehistoric grasslands were dominated by annual forbs rather than grasses (Blumler, 1992, 1995; Hamilton, 1997; Holstein, 2001; Minnich, 2008; Schiffman, 2000, 2007; Wester, 1981). Phytolith evidence supports Minnich's (2008) contention, based on accounts of early explorers in the Central Valley, including Zalvidea, Moraga, Fremont, and Muir, that at the time of European contact, this region was open prairie largely characterized by annual forbs producing

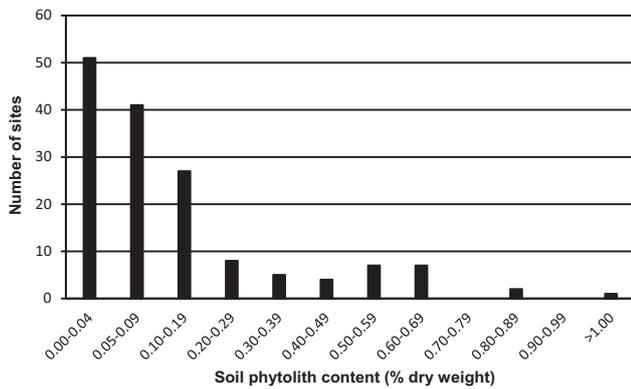


Figure 2. Frequency distribution of soil phytolith content for 153 Californian grassland sites.

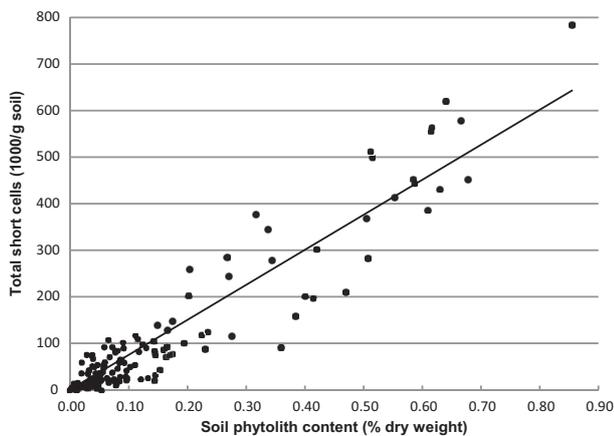


Figure 3. Total short cell phytoliths as a function of soil phytolith content for 153 Californian grassland sites.

magnificent wildflower displays rather than grasses. In contrast, accounts from early Spanish exploration of coastal California described prairies composed of bunchgrasses interspersed with wildflowers maintained by frequent Native American burning, which also agrees with phytolith evidence for this region. In an attempt to reconstruct prehistoric species composition, a study of plant species data from 13 relict grassland preserves found 1348 species; nearly 50% were annual forbs occurring at only one or two sites (Schiffman, 2007). Percentage of perennial grass species increased with increasing precipitation, while annual forb species increased with decreasing precipitation, in accord with historical and phytolith data. Because shrubs, like forbs, produce very few phytoliths, phytolith analysis is not able to distinguish forb-dominated from shrub-dominated sites. Low soil phytolith content combined with relict analysis suggests that some regions, particularly parts of the southern San Joaquin Valley, may have been dominated by shrubs rather than forbs.

There are several issues to consider when interpreting the phytolith evidence and its implications. Soil phytolith content at a site in California is affected by many factors, including the percentage of grass or other phytolith producing plants in the vegetation type, the length of time that type has occupied the surface, the presence and depth of bioturbation and other disturbances, soil depth and texture, and climate (Evetts et al., 2012). Because the geographical distribution of Californian grasslands have probably been largely stable during the Holocene, the climate throughout the grassland region is Mediterranean, bioturbation is ubiquitous and sites identified by phytolith analysis as grass-dominated do not appear strongly correlated with soil depth or texture (data not shown), the

most likely explanation for differences in observed soil phytolith content in California is the percentage of grass in the long-term vegetation; soil phytolith content is probably an indicator of long-term grass cover. Phytolith content in most Great Plains long-term grassland soils is >1%, but only two sites in our study had phytolith content >0.7%. Although climatic factors clearly play a role, the differences in typical phytolith content may indicate that prehistoric Californian grass-dominated grasslands had substantially more forb cover than their Great Plains counterparts.

Time required to accumulate the observed phytolith assemblage is an important consideration when using soil phytolith content to estimate long-term vegetation at a site. The near-surface soil phytolith assemblage is the result of many years of phytolith deposition, weathering and dissolution processes. Radiocarbon dating carbon occluded in phytoliths to estimate the mean residence time of phytoliths in the soil has proven problematic (Santos et al., 2010). Estimates based on the annual biogenic silica input for annual grassland in northern California found the minimum time required to accumulate 0.30% phytolith content in the upper 60 cm of soil under grass-dominated vegetation was 450 years (Evetts et al., 2012). Because considerable biogenic silica produced by grasses is poorly silicified and rapidly dissolved in the soil (Blecker et al., 2006), the actual time required to accumulate 0.30% phytoliths is likely several times longer, suggesting the phytolith assemblage in highly bioturbated soils commonly seen in California is the result of at least 1000 years of accumulation. Inputs due to changes in vegetation (including exotic annual grass invasion and the arrival of agricultural crops) that occurred during the <200 years between European settlement and the collection date of soil archive profiles are unlikely to have substantially changed the soil phytolith assemblage. Supporting this assertion, we found that soil at many sites now converted to annual grassland or crops contained relatively high content of bilobate phytoliths, which could only have been deposited by native grasses prior to conversion.

High correlation between grass short cell counts and soil phytolith percent weight (Figure 3) indicates that most phytolith input on Californian grassland comes from grasses, confirming the results of limited studies of phytolith reference material from widespread Californian species (Evetts et al., 2006). Although soil phytolith content, like plant species cover, is a continuum, the $\geq 0.3\%$ soil phytolith weight threshold used to classify sites with substantial grass cover in California (Evetts et al., 2012) is a useful dividing line for discussing relative importance of grass at a site. This threshold corresponds to $\sim 200,000$ total grass short cells/g soil (Figure 3). Even though soil phytolith percent weight produces good estimates of long-term grass cover in California, we believe that absolute counts of grass short cells (which require only one additional hour of analysis time per site) are more robust, unequivocal indicators of long-term grass cover, particularly for vegetation types where non-grass species provide considerable input to the soil phytolith assemblage, and should become a standard measure used for quantitative soil phytolith analysis.

The limited extent of prehistoric grass cover in California suggested by the phytolith data may be due to unusual aspects of the Mediterranean climate. The availability of summer moisture, typically restricted to locations with substantial summer fog, a high water-table or summer thunderstorms in California, may be an important requirement for extensive native perennial grass cover (Clary, 2012). Recent research on the Iberian Peninsula suggests that the extreme lack of summer dry season precipitation that typifies California's Mediterranean climate strongly favours annual grasses compared to perennial grasses (Clary, 2008); perennial grasses are likely not dominant in California because of severe summer drought. However, Hamilton et al. (1999) found that periods of winter drought, commonly experienced in California, have strong negative effects on annual grasses, possibly

explaining why California's native annual grass flora is depauperate compared to the Mediterranean region. Native annual forbs appear better adapted than native grasses to the environment created by the unique characteristics of California's climate.

Our results have important implications for restoration and management of Californian grasslands. In the absence of hard data on pre-European settlement reference conditions, many grassland restoration projects have by default focused on increasing cover of native perennial grass species, particularly *Stipa pulchra* (Stromberg et al., 2007). Our data suggest that considerable money and effort are being wasted at many sites because they likely never supported substantial cover of native grasses. Phytolith analysis provides the means to estimate prehistoric grass cover at a site and establish a realistic species composition target to plan for and monitor the success of a restoration project. We believe grassland restoration projects in California and elsewhere should routinely employ phytolith analysis in conjunction with historical source analysis early in the planning stage (Evelt et al., 2012).

Conclusion

Phytolith analysis is a simple, economical, palaeoecological tool that provides direct evidence of prehistoric grassland ecosystems. Analysis of surface soil phytolith content from a statewide archive of soil profiles strongly indicates that most prehistoric Californian grasslands were not dominated by grasses. There is no evidence that large areas of prehistoric Central Valley grasslands had substantial cover of *Stipa pulchra*. Combined phytolith, historical account and relict analysis evidence indicate that the extent of prehistoric Californian grassland was similar to modern CAG extent, but individual species cover was likely highly patchy, reflecting small-scale environmental heterogeneity. Although there were likely limited areas dominated by grasses or shrubs, most non-coastal regions were probably dominated by an unusually diverse assemblage of native annual forb species occupying narrow environmental resource niches.

Prior to initiating restoration of grassland sites in California, soil phytolith analysis should be performed to avoid costly attempts to establish grasses in areas where they were not prehistorically abundant. Additional research utilizing quantitative phytolith morphotype analysis may enable identification of native grasses to the genus or species level, providing further useful information for restoration efforts.

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