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A 55,000 Year History of California Plant Community and Ecological Response to Climate

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A 55,000 Year History of California Plant Community and Ecological Response to Climate

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in Geography

by

Jessie Rachel George

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ABSTRACT OF THE DISSERTATION

A 55,000 Year History of California Plant Community and Ecological Response to Climate

by

Jessie Rachel George

Doctor of Philosophy in Geography

University of California, Los Angeles, 2022

Professor Glen Michael MacDonald, Chair

Plant macrofossils can be powerful proxies for environmental change, but their preservation in the fossil record does not always allow for long-term reconstructions. The La Brea Tar Pits are unique not just for the sheer abundance of fossils they preserve from the Late Pleistocene and Holocene, but also for the particular taphonomic conditions that allow for continuous preservation of an ecologically diverse fossil assemblage across a 55 ka timespan (Chester Stock, 1992). This proves especially valuable in the Mediterranean region of coastal Southern California, where long-term terrestrial records are spatially scarce (Glover et al., 2020; Kirby et al., 2018). Hydrocarbon preservation of cellulose and lignin allows for the preservation of plant macrofossils (fossils visible with the naked-eye and identifiable using low-magnification microscopy) which have the potential to provide species specific data on plant presence through time (S. T. Jackson et al., 1997). Rich ecological data through the Late Pleistocene and Holocene provides much needed information on how plant communities were responding during a climatically active time of glacial growth and decline, and millennial-scale shifts in atmospheric and sea surface temperatures (SST), as well as important environmental context for development and the extinction of Ice Age megafauna and migration of human populations (Barnosky et al., 2017; Meltzer, 2020).

This dissertation explores the viability of La Brea Tar Pit plant macrofossils as environmental and plant community proxies. Through active seep observation and exploration of taphonomic processes of plant deposition in modern hydrocarbon seeps, multi-method approaches to identification, and direct accelerator mass spectrometry (AMS) radiocarbon dating of preserved plant material, this project constructs a high taxonomic resolution, 55 ka long, record of vegetation change for the Los Angeles Basin. This dissertation finds plant material deposition in asphalt seeps to be highly localized and representative of flora fruiting in warmer months. Through the La Brea Tar Pits vegetation record we have found species response in the Los Angeles Basin to be sensitive to climatic changes driven by orbital forcings, and potentially variations in the Northeast Pacific and North Atlantic sea surface temperatures. Substantial changes in the flora and vegetation cover are recorded in the LBTP record and some of these shifts are contemporaneous with local extinction of mega-fauna both during the transition from the Pleistocene to the Holocene (Marine Isotope Stages MIS2 to MIS1 - ~12 ka) and in the earlier Pleistocene. The disappearance of large-bodied herbivores at the start of the Holocene, coupled with increased fires, possible increasing in frequency due to the arrival of humans, potentially also played a role in the vegetation changes observed, most notably the extirpation of

juniper from the Los Angeles Basin. This local-scale record of environmental shifts from the Late Pleistocene into the Holocene at the LBTP's provides a dynamic baseline of plant species presence for future environmental and ecological studies of paleo-coastal Southern California, and possibly assessing the sensitivity of current vegetation to ongoing and future climatic changes.

This dissertation of Jessie Rachel George is approved.

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George, J., MacDonald, G. (2019, February 17th-20th) *Plant Community Shifts at the La Brea Tar Pits Throughout the Late Pleistocene in Relation to Climate* [Poster]. PACLIM 2019, Pacific Grove, CA, USA. https://sites.google.com/site/paclimconference/paclim-2017/paclim-2019?authuser=0

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Chapter 1 Introduction

Coastal Southern California, a biodiversity hotspot where a diverse fauna and flora face increasing environmental pressures and anthropogenic threats, is also home to one of the richest paleontological records for the Late Pleistocene and Holocene. The La Brea Tar Pits (LBTP) fossil deposits in Los Angeles, California, is so prolific in its preservation of Ice Age life that it became the namesake of the Rancholabrean North American Land Mammal Age of the Late Pleistocene (Bell et al., 2004). Hundreds of thousands of LBTP asphalt impregnated fossil bones of Ice Age megafauna have been excavated at the site since the turn of the last century. These fossils have contributed hugely to our current understanding of the life histories and ecologies of charismatic fauna like mammoths, dire wolves, and sabertoothed cats (Adli et al., 2015; Akersten et al., 1988; Balisi & Van Valkenburgh, 2020; Binder et al., 2002; Brown et al., 2017; Chester Stock, 1992; Coltrain et al., 2004; DeSantis et al., 2019; Feranec et al., 2009; O'Keefe et al., 2022). They are, however, only a fraction of the larger fossil assemblage present in the LBTP deposits. Insect chitin, calcium-carbonate shell, small vertebrates, and plant cellulose and lignin are all readily preserved by seep hydrocarbons (Chester Stock, 1992; Fox et al., 2019, 2022; Gerhart et al., 2012; Glover et al., 2018; Holden et al., 2014, 2015, 2017; Holden & Harris, 2013a; Holden & Southon, 2016a; Mychajliw, Rice, et al., 2020; Ward et al., 2005; Warter, 1976). These less well studied fossils can offer far more environmental context than their large mammal counterparts. Among these, plant fossils, are extremely powerful proxies for environmental change and have the potential of filling large gaps in our knowledge of important environmental changes of the past ~55 ka years.

The climatic stability that has defined our planet's recent past millennia has provided us with a revealing backdrop to the magnitude of human driven change currently influencing our global climate patterns. Anthropogenic climate shifts and land use in recent history have had a noticeable impact on extinction rates, species distribution, plant community productivity, as well as overall biodiversity, prompting the characterization of the modern period as a ‘6th extinction’ (Barnosky et al., 2011). While the anthropogenic origin of our current climatic and ecological instability is novel, the scenario of widespread environmental change and species loss is not. Periods of rapid and appreciable loss of species have occurred in the past, including at the end of the Pleistocene. Understanding the drivers behind these ecological turning points has the potential to provide us with a deeper understanding of the environmental thresholds and resiliency of our modern terrestrial and marine systems (Barnosky et al., 2017; Willis & MacDonald, 2011).

The Late Pleistocene and Holocene periods represented in the LBTP’s fossil deposits saw great climatic and ecological change. The last great glaciation of the continent and the transition to our current warm interglacial which saw shifts in temperature and atmospheric carbon similar to modeled predictions of the 21st century (Willis & MacDonald, 2011). Millennial-scale events impacting atmospheric temperatures and SST are recognizable off the coast of California and in surrounding regional records (Glover et al., 2017a, 2020; Hendy, 2010; Hendy & Kennett, 2000; Heusser, 1998, 2000; Kirby et al., 2006). Notably, the most recent mass extinction began in the Late Pleistocene, and despite its temporal proximity, a surprising amount of uncertainty remains surrounding its drivers. A startling proportion of the earth’s large-bodied mammals (mammals weighing over 40 kg), including 34 genera in North America, disappeared by 10 ka (10,000 calendar years before present) (Barnosky & Lindsey, 2010; Gill et al., 2009; Koch & Barnosky, 2006; O’Keefe et al., 2009). This period also witnessed the introduction of humans into North America (Becerra-Valdivia & Higham, 2020; Bennett et al., 2021; Meltzer, 2020).

A 2020 review of Quaternary extinction literature by David J. Meltzer, identifies key areas that need to be addressed to better understand what challenges species faced at the end of the Pleistocene. This includes the speed and magnitude of changes to temperature, precipitation, and seasonality during the last transition from glacial to interglacial for comparison to previous periods of transition. A need for more data on the functioning of ecological communities throughout this period including their makeup, diversity, and productivity. A thorough investigation of the drivers behind the Late Quaternary extinction requires an examination of the event from the lowest trophic levels up (Gill et al., 2009; Gill, 2014; Jeffers et al., 2018; MacDonald et al., 2012; Perrotti, 2018). Incorporating vegetation based studies with higher taxonomic and spatial resolution is a necessary step towards addressing the outstanding gaps in our knowledge of the Late Pleistocene environmental changes (Jeffers et al., 2018; Meltzer, 2020; Stuart & Lister, 2012).

Palynological records have been a prolific contributor to our understanding of changing vegetation in the Quaternary Period but can present limitations in both taxonomic and spatial resolution. To effectively address the questions remaining surrounding Quaternary extinctions a wide range of proxies need to be employed to supplement faunal and pollen datasets. Plant macrofossils (fossils visible with the naked eye and identified using low-magnification microscopy) can be a powerful tool in this endeavor. While spatial representation will vary on a site-by-site basis, the increased mass of plant macrofossils generally limits distance of travel compared to pollen grains. They can also provide taxonomic identifications to the genus and species level allowing for more detailed reconstructions of local plant community dynamics (Birks, 2017; Follieri, 2010; Jackson & Weng, 1999). A challenge represented by plant macro-fossil records is their lack of abundance in many long-term records such as sediment cores, and tendency to represent occasional single time slices, rather than continuous records. The LBTP fossil assemblage offers a rare opportunity to examine vegetation change across a ~55 ka time period with plant macrofossils in a region where aridity makes more common environmental records like lake cores spatially sparse. The potential abundance of plant macrofossils in the sediments of the LBTP, coupled with the potential of Accelerator Mass Spectrometry (AMS) radiocarbon dating to provide ages for large numbers of such fossils, provides the opportunity to develop an important, long and continuous record of local vegetation at this internationally important site.

This project provides a baseline of vegetation change at LBTP through fossil identification and AMS radiocarbon dating of individual plant fossils from the LBTP sediments. As a prelude, the taphonomy of such sites is considered through a study of a modern set of seeps. The guiding general questions behind this dissertation are:

1) How do asphalt seep taphonomic processes influence plant species representation? What is the degree of spatial distribution represented within the LBTP asphalt seeps? Is there seasonal or species-based bias?
2) Does flora from LBTP reflect climatic and environmental changes observed in nearby regional records, do species level records reveal more subtle patterns?
3) Do shifts in vegetation relate to larger climatic and ecological changes coincidental with extinction of megafauna and initial presence of human beings?

The dissertation is separated into 3 chapters. Chapter 2, **Taphonomic Observations from Small Tar Seeps in Southern California**, explores taphonomic processes associated with plant entrapment in two seeps in Santa Clarita, California, through year-long monitoring of atmospheric and seep temperature. Seep activity is monitored through timelapse imagery to exam seep flow and plant and animal interaction throughout the year. Plant line-transect surveys of the area surrounding seeps are coupled with seep surface samples to understand spatial representation and seasonal bias. Chapter 3, **Identification of Fossil Juniper Seeds Preserved in La Brea Asphaltum Deposits: Implications for Climate Change and Drought in the Late Pleistocene**, develops a multi-facted methodology used in the identification of a previously unidentifiable fossil juniper commonly found in LBTP deposits, 2D image analysis, 3D computed tomography, and species distribution models. AMS radiocarbon distributions of the previously unidentified species are compared to distributions of fossil *Juniperus californica* to better resolve and understand past environmental shifts at LBTP. Chapter 4, **A 55,000 Year History of California Plant Community and Ecological Response to Climate**, presents the reconstructed chronology of plant species presences at LBTP. With 26 taxa and 188 AMS radiocarbon dates. The plant macro-fossil record is compared to patterns of late Pleistocene – Holocene climatic change, extinction of the mega-fauna and the initial arrival of humans.

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Chapter 2 Taphonomic Observations from Small Tar Seeps in Southern California

2.1 Abstract

La Brea Tar Pits is one of the richest Ice Age fossil localities in the world and offers unmatched potential for reconstructing environmental conditions and ecological relationships in the Late Pleistocene. However, accurate interpretation of environmental proxies like plant macrofossils requires a better understanding of the processes behind their deposition in hydrocarbon seeps and potential for spatial mixing, a topic not yet addressed in asphalt pit related research. In this study we monitor temperature, plant growth, and seep activity of two hydrocarbon seeps in different depositional contexts over the span of a year. For each seep we surveyed surrounding vegetation to a distance of 10 meters and sampled seep surfaces for analysis of trapped plant material. We find hydrocarbon seeps to be highly localized with 77-91% of plant material originating from species found within 5 meters of the seep. Temperature and timelapse imagery indicate a higher likelihood of transportation of plant material by wind or animal than by water in these particular seeps. Animal transport through fecal matter or entrapment was the most likely candidate for the species (Sambucus nigra) transported from outside the immediate vicinity of the monitored seeps. Variation in visible seepage of liquid asphalt correlated with seasonal temperature changes, with higher temperatures coinciding with increased seep flow. We find observations of seasonal seep flow connected to a warm season bias of plant material, making phenology an important consideration in the interpretation of plant presences in asphaltic fossil contexts.

2.2 Introduction

La Brea Tar Pits (LBTP) is an internationally recognized Lagerstätte on the Southern California (USA) coast known for its prolific preservation of a diverse range of Pleistocene fossil material. Miocene period oil-bearing rock beneath the surface of LBTP has been the source of surficial hydrocarbon pooling for the past 60 ka. The sticky asphalt pools that formed on the surface acted as traps for Ice Age mammals like mammoths, freshwater mollusks, insects, and seeds, cones, and leaves. The exquisitely preserved bone, chitin, shell, and plant material provides valuable insight into past fauna, flora, and environmental and ecological shifts of the past 60,000 years (Gerhart et al. 2012; Holden et al. 2014; DeSantis et al. 2019). Plant remains can be sensitive indicators of environmental conditions and provide an important context to interpret faunal remains. However, interpretation of plant fossil assemblages present in the LBTP deposits requires a greater understanding of the taphonomic processes specific to their deposition and preservation in hydrocarbon seeps. The degree of spatial mixing of local and extra-local plant species and temporal mixing within deposits is difficult to assess at LBTP, as the original sedimentary stratigraphies commonly aren't preserved, and thus chronological reconstructions are primarily dependent on radiocarbon dates from individual specimens (Friscia et al. 2008; Holden et al. 2017). Past efforts to understand LBTP taphonomy have focused on the entrapment of Pleistocene megafauna and the role of hydrocarbon seeps at LBTP as carnivore traps for predators and scavengers (Merriam 1911; Shaw and Quinn 1986; Chester Stock 1992; Spencer et al. 2003; Carbone et al. 2009; McHorse et al. 2012). Decomposition and movement of faunal material post-deposition has been a focus of some previous work that has yielded valuable information about the disarticulation and mixing of fossils after burial (Friscia et al. 2008; Holden et al. 2013; Brown et al. 2017), but little attention has been paid to patterns of plant deposition and representativeness.

Plant fossils provide evidence of faunal food sources and habitats and can be powerful proxies for climate. Plant macrofossils, fossilized material that can be seen with the naked eye and identified using low-magnification microscopy, are particularly informative in this regard as they are more likely to be of local origin than palynomorphs and can more frequently be identified down to the species level (Jackson et al. 1997; Jackson & Weng 1999; Follieri 2010). The advent of AMS radiocarbon dating allows for age determinations of plant macrofossils such as individual seeds or leaves that was previously impossible at the LBTP. The preservation of plant macrofossils also provides opportunities for analyses of leaf cell configurations and stable isotopes, linking data on climate, productivity, and nutrient cycling directly to plant remains (Ward et al., 2005; Gerhart et al., 2012; Dunn et al., 2015; Birks, 2017; Tahmasebi et al., 2018; Milligan et al., 2021). As most late-Quaternary plants are still extant, modern distributions of species can be used to infer past environmental conditions individually or through multi-species models (Blois et al. 2013; Harbert & Nixon 2018; Lora & Ibarra 2019). The rich preservation of plant fossil material, including seeds, leaves, needles and wood fragments, at LBTP has great potential for addressing important questions about local and regional climate and ecology during the Late Pleistocene and Holocene.

Understanding the degree of spatial mixing and geographic representativeness for plant fossils is of great importance when using species assemblages as proxies to inform environmental and ecological reconstructions in a heterogenous landscape like Southern California. Topographic and geologic differences can make a small difference in location yield substantially different environmental conditions and vegetation. The plant macrofossil representation at a single site is the result of interrelationships between landscape, phenology, reproduction and dispersal mechanisms, as well as the mechanics of deposition and preservational biases. Lessons learned from plant macrofossils in lacustrine environments offer some insight: In lakes, swamps, and similar low energy environments, the larger size and increased weight of plant macro-remains generally limits their transport locally compared to material like pollen. Wind, water, animals, storms, fire, runoff, and even avalanche activity all have the potential to deposit plant macro-remains, but wind and stream activity are primarily responsible for the movement of plants over longer distances (Birks 2002, 2017). The more localized distribution of plant macrofossils mean that differences in sampling location even within the same lake may account for differences in community representation (Heggen et al. 2012) suggesting that contemporary hydrocarbon seeps in close proximity may see differences in species assemblage from one seep to the next.

Delineating relationships between plant fossil assemblages preserved in hydrocarbon seeps and contemporaneous surrounding flora requires understanding the seep-specific processes taking place, such as the effect of seasonal differences in temperature on seep viscosity and ability to trap plant material or the influence of plant and animal activity on seep species representation influenced by seasonal patterns and seed dispersal mechanisms. To this end, knowledge of the full suite of plant species growing around the site of deposition and their respective life histories is necessary to establish not just species presence but also absence and the processes behind the representational bias.

This paper will examine hydrocarbon seep specific taphonomic processes involved in the deposition of plant macrofossil material at two modern hydrocarbon seeps (figure 2-1) located ~40 km NW of the La Brea Tar Pits. We integrate survey of plant distribution in the vicinity of the seep and the plant content in the surface asphalt with a year-long photo-monitoring study of

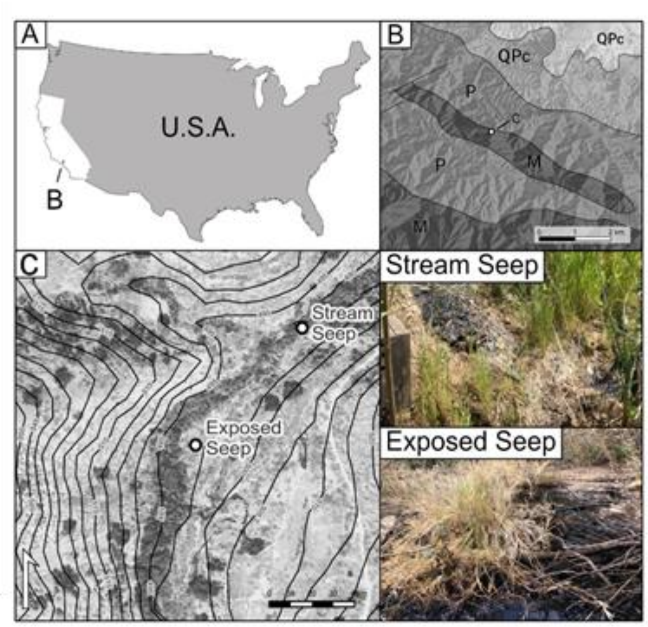

Figure 2-1: Map of Towsley Canyon with seep sites. A) Site location within contiguous USA B) Site location (C) on edge of Miocene (M) age, marine sedimentary Modelo Formation on the border of a Pliocene marine sedimentary rock and non-marine Pliocene and/or Pleistocene (P) sedimentary deposits (reproduced with permission from "Geologic Map of California", Charles W. Jennings et al., 2010, California Geological Survey. C) monitored exposed and stream asphalt seep sites within Towsley Canyon.

activity at the seeps and monitoring of air and asphalt temperatures. This study uses these data to examine how seep temperatures vary with seep activity and entrapment capacity over the course of a year, and what if any spatial or temporal bias in plant material is reflected in seep composition.

2.2.1 Methods

Two seep sites at 34.352071 N, -118.579804 W and 34.352612 N, -118.579360 W were monitored, surveyed, and sampled from June 2018 to June 2019. The seeps lie in Towsley Canyon in the Santa Susana Mountains (part of the Transverse Ranges) within the ancestral and unceded territory of the village of Tochonanga and the people of the lineage Tochonabit, whose descendants are citizens of the Fernandeño Tataviam Band of Mission Indians. Both hydrocarbon seeps are located atop the Miocene age Modelo Formation that supported active oil extraction in the area from the mid-1800s until the 1990s (Levin 1992; Squires 2012). The site today is partially disturbed, with a mix of native and invasive flora, a year-round stream and active hydrocarbon seeps. The area receives annual rainfall amounts of 417 mm, a mean temperature of the warmest quarter of 23.75°C, and mean temperature of the coldest quarter of 10.62°C according to the WorldClim climate database (averaged from the years 1970-2000) (Fick & Hijmans 2017).

Sites were selected to represent a diversity of possible scenarios for plant material deposition. The first stream seep is located on the streambank at the canyon bottom with some riparian canopy cover, and the second exposed seep is situated on a flattened terrace on the hill above, surrounded by chaparral scrub.

For site specific temperature records a HOBO pendant temperature data logger recorded atmospheric temperature in the area surrounding the two seeps over the course of a year. The sub-surface seep temperature (~2.5 cm below the seep surface) of both locations was monitored and recorded over the same period with submerged pendant loggers. Phenological patterns in surrounding flora and faunal activity around the seeps was monitored with camera traps set to capture one image at peak temperature each day and additionally when triggered by motion in or around the seep.

Three 10-meter line transects were sampled for vegetation, radiating from the edge of each seep to record plant species growing in proximity. Surface asphalt samples of approximately 475ml were taken from each seep to a depth of 50 mm to compare seep plant fragment contents to the flora immediately growing around the seep. Surface samples were cleaned with repeated washes in a 2:1 toluene: methanol solution in a sonication bath to extract and identify trapped plant material. Plant material was identified under a stereoscopic microscope using reference material collected in the field the UCLA Herbarium.

General phenology and local fruiting periods were determined through the flowering and fruiting observations on iNaturalist coupled with a search of digitally scanned Herbaria specimens specific to Los Angeles County from the California Consortium of Herbaria (CCH2) online portal for more location specific phenological patterns. Online databases of herbaria collections and “Citizen” or “Community Science” observations have proven robust and accurate sources of phenological data (Mayer 2010; Fuccillo et al. 2015; Willis et al. 2017).

2.3 Results

2.3.1 Air and Seep Temperature

Air temperatures at the site saw extremes ranging from a minimum of -4.5°C in January to a maximum of 52.6°C in August with a year-long average of 17°C. Recorded site temperature maximums greatly exceed the nearest weather station ~7 km away, which recorded a maximum temperature of 46.67°C (weather station Ew9895 in Porter Ranch). Minor differences in temperature to surrounding averages can result from slope aspect in the surrounding canyon (Burnett et al., 2008). The increase of 5.93°C observed here is likely a product of the natural foliage used to shade the logger shifting, exposing it to direct solar radiation. Subsurface temperatures of the stream seep were on average 3.2°C warmer than air temperatures with temperature extremes ranging from 1.3°C to 56.4°C. Fluctuations in the daily temperatures of the stream seep are constrained in the winter season as the stream level rises and the seep is periodically covered in water, bringing temperature minimums and maximums together as the water temperature remains more stable than the air (Figure 2-2). Subsurface seep temperature in the exposed seep were on average 3.7°C higher than the stream seep and 6.9°C greater than air temperature with extremes ranging from -2°C to 69.6°C.

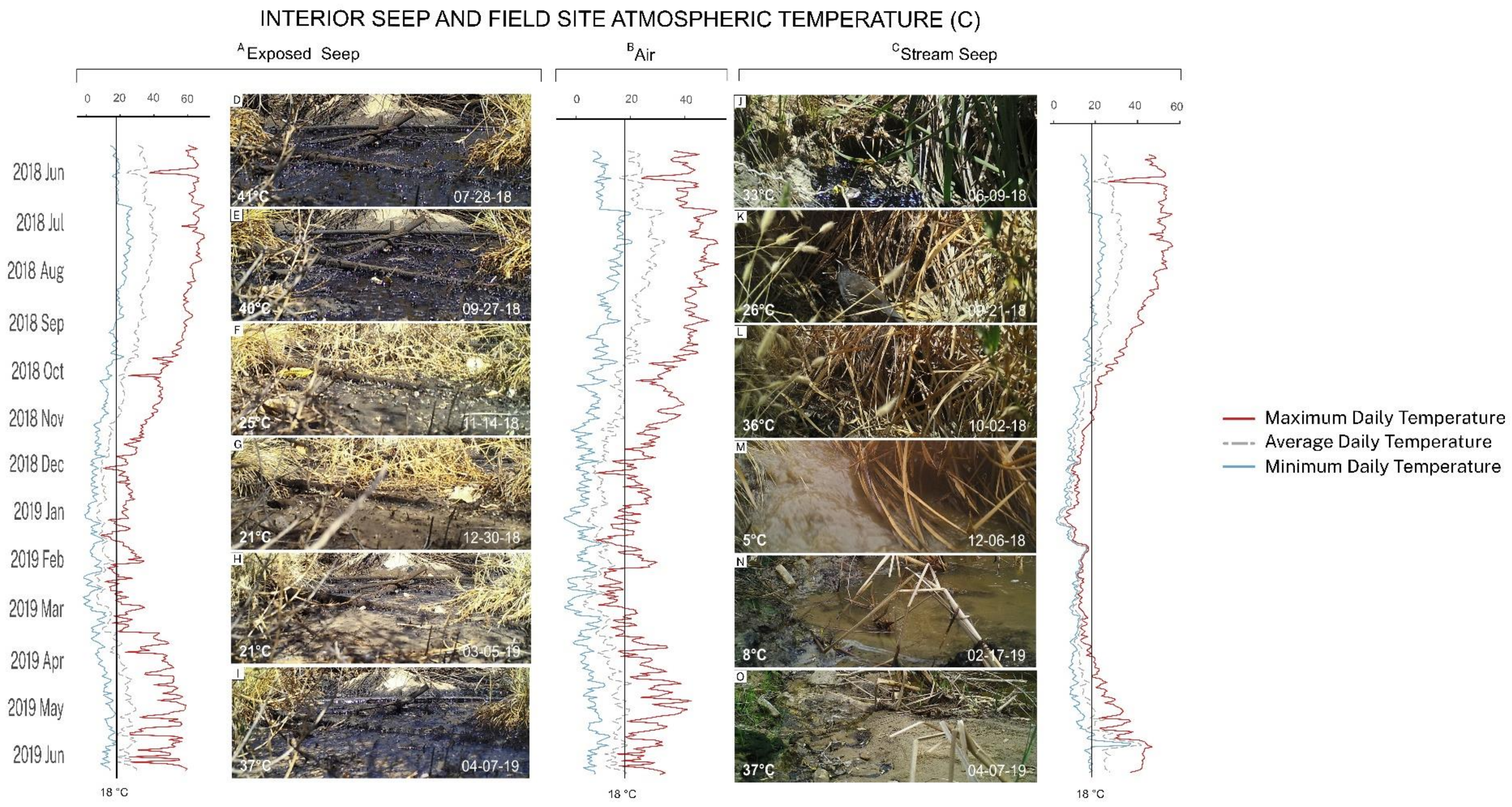

Figure 2-2: Site specific temperature records (Celsius) from temperature logging pendants of A) ~2mm below the exposed seep site B) atmospheric temperature (air), and C) ~2mm below surface of the stream seep. Red line = maximum temperatures, grey dashed line = temperature averages, and the blue line = minimum temperatures. D-I) Timed photographs of exposed seep taken at 1pm in July, September, November, December, March, and April. J-O) Time photographs of stream seep taken at 1pm in June, September, October, December, February, and March.

2.3.1.1 Observations from Cameras

Stream seep cameras captured the seasonal periodic submersion of the seep by the heightened flow of the stream in winter, followed by growth of vegetation around the seep in late spring and summer. Most notably the development of *Polypogon monspeliensis* inflorescences in June and the abrupt shedding of seed spikelets in mid-October. Liquid asphalt appears to resume active seepage to the surface in June and July, indicated in the photographs by the replacement of accumulated surface sediment with glossy black asphalt. California Thrashers (*Toxostoma redivivum*), Virginia opossums (*Didelphis virginiana*), and a gray fox (*Urocyon cinereoargenteus*) were observed walking on the seep at night in September, when nighttime and early morning temperatures dipped below 18°C, without entrapment (Figure 2-3D-F). Patterns of seep activity were harder to discern with fluctuating stream activity and continued deposition of sediments on the seep surface.

The exposed seep recorded similar growth patterns of *Distichlis spicata* as *P. monspeliensis* in the stream seep. Inflorescences appeared to bear fruit between late July and mid-October. The exposed seep appears at its most viscous in August and September. In mid-October, sediment collected on the seep surface suggesting less seep activity. Sediment and plant material continue to build up on the surface until after April when surface material disappears with renewed seep activity. Seep activity appears to be limited to periods with sustained temperatures of 20°C and above. Animal activity is recorded on the surface of the exposed seep at night from November to January. A mouse (*Peromyscus* sp. or *Reithrodontomys* sp.) and woodrat (*Neotoma* sp.) can be seen regularly walking the surface of the seep from 2:00-6:00 AM in the morning (Figure 2-3A,B). The smaller of the two is recorded on the seep as early as late September.

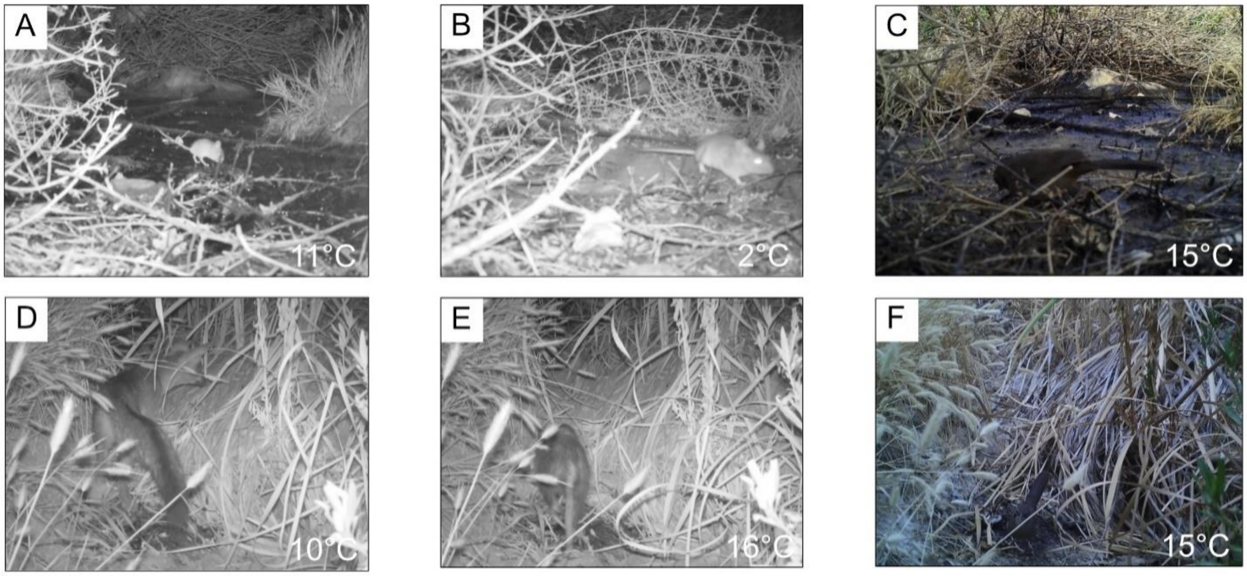

Figure 2-3 – Fauna captured by motion triggered camera trap A-C: Exposed seep (A) A mouse (*Peromyscus* sp. or *Reithrodontomys* sp.) walks on the surface of the seep 1:53 am September 5th, 2018 (B) A woodrat (*Neotoma* sp.) on the seep surface 4:23 am January 1st, 2019 (C) A California Towhee (*Melozone crissalis*) on or near the seep 2:50 pm March 1st, 2019 D-F: Stream seep (D) Gray fox (*Urocyon cinereoargenteus*) passes over stream seep 5:46 am September 4th, 2018 (E) Virginia opossum (*Didelphis virginiana*) 10:42 pm September 7th, 2018 (F) California Thrasher (*Toxostoma redivivum*) standing on top of the seep at 8:16 am September 8th, 2018.

2.3.1.2 Plant Survey

Three 10-meter line transects radiating from the stream seep were sampled with bearings of N 43° W, N 76° E, and S 45° W (Figure 2-4B). Both Northeast and Northwest transects see transitions from primarily riparian species to more xeric scrub/chaparral associated species as their paths move uphill away from the streambed. The Southwest transect that runs upstream parallel to the bed, is dominated by riparian species. *P. monspeliensis*, *Salix* sp., and *Typha latifolia* lie closest to the seep, ranging from 0 to 2 meters in the NW and NE transects. *Baccharis salicifolia* is dominant ranging from 2-4 meters away in all directions, accompanied

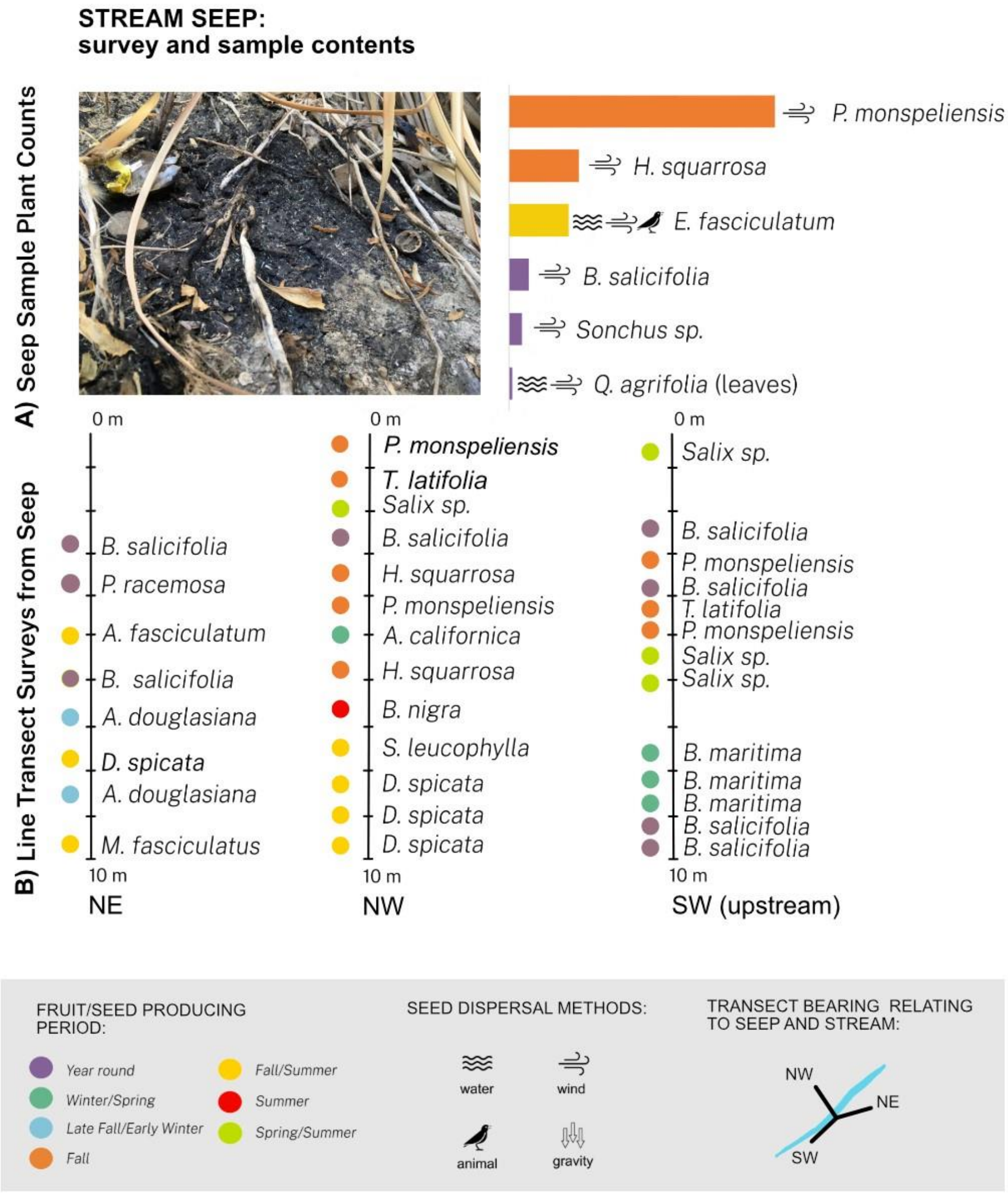

Figure 2-4— Results of survey and surface sampling for the stream seep. **A)** Plant material identified from surface sample **B)** Results of the 3 line transect surveys radiating to the NW, NE, and SW. Fruiting season is indicated by color and seed dispersal mechanisms by icon. Bird icon by Iconic, down arrow by Fix Project, wind by Fahmihorizon, water by Ainsley Agatha from the Noun Project.

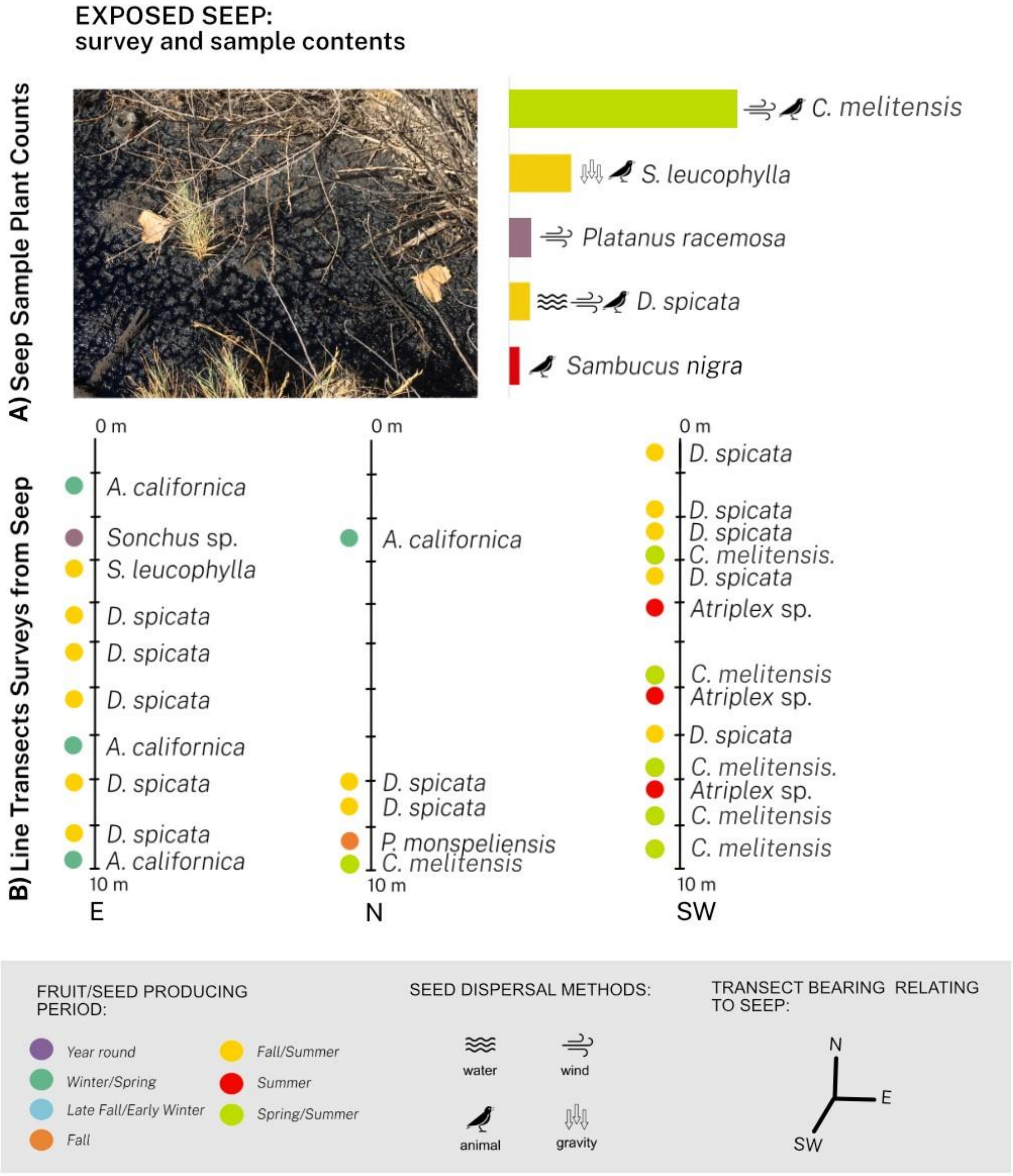

Figure 2-5 — Results of survey and surface sampling for the exposed seep. **A)** Plant material identified from surface sample **B)** Results of the 3 line transect surveys radiating to the NW, NE, and SW. Symbols the same as Figure 2-4.

by *Hazardia squarrosa* in the NW transect, *Platanus racemosa* in the NE transect, and *P. monspeliensis* in the SW (upstream) transect. From 4-6 meters from the seep *Adenostoma fasciculatum* and *B. salicifolia* are present to the NE, *P. monspeliensis, Artemisia californica,* and *H. squarrosa* to the NW, and *T. latifolia, P. monspeliensis,* and *Salix* sp. to the SW. From 6-8 meters from the seep, *Artemisia douglasiana* and *D. spicata* are present to the NE, *Brassica nigra* and *Salvia leucophylla* to the NW, and *Salix* sp. and *Bolboschoenus maritima* to the SW. From 8-10 meters from the seep *A. douglasiana* and *Malacothamnus fasciculatus are* present to the NE, *D. spicata* to the NW, and *B. maritima* and *B. salicifolia* to the SW.

Three 10-meter line transects radiating from the exposed seep were sampled with bearings of N 1° W, N 88° E, and S 24° W (Figure 2-5B). All transects are dominated by primarily xeric species and have higher proportion of open ground compared to the stream seep. Directly surrounding the exposed seep from 0-2 meters there is *A. californica* to the E, bare ground to the N, and *D. spicata* to the SW. From 2-4 meters there is *S. leucophylla* and *D. spicata* to the E, *A. californica* and bare ground to the N, and *D. spicata* and *Centaurea melitensis* to the SW. At 4-6 meters there is *D. spicata* to the E, bare ground to the N, and *Atriplex* sp. and *C. melitensis* to the SW. At 6-8 meters *D. spicata* and *A. californica* to the E, bare ground to the N, and *Atriplex* sp., *D. spicata,* and *Centaurea* sp. to the SW. At 8-10 meters *D. spicata* and *A. californica* to the E, *D. spicata, P. monspeliensis,* and *C. melitensis* to the N, and *Atriplex* sp. and *C. melitensis* to the SW.

2.3.1.3 Surface Samples

The surface sample taken from the stream seep (Figure 2-4A) yielded a total of 149 specimens comprising 8 plant taxa, 5 of which were identifiable to species. Sample makeup is composed of 88 *P. monspeliensis* spikelets, 21 *H. squarrosa* cypselae, 18 *Eriogonum* *fasciculatum* achenes and 4 inflorescence fragments, 6 *B. salicifolia* cypselae, 5 *Quercus agrifolia* leaf fragments, 4 cypselae of *Sonchus* sp., and 3 seeds of two unknown taxa. 5 specimens of disassociated insect chitin were also present in the sample.

Surface samples taken from the exposed seep (Figure 2-5B) yielded only 33 specimens comprising 5 plant taxa, 22 *C. melitensis* cypselae, 4 *S. leucophylla* nutlets and 2 leaves, 1 *Sambucus nigra* ssp. *caerulea* seed, 1 cypsela and leaf fragment of *Platanus racemosa*, and 1 seed and inflorescence fragment of *D. spicata*. The exposed seep sample was notable for containing a high representation of faunal material with a high density of insect chitin, feathers, fur, rodent and bird bones.

2.4 Discussion

2.4.1 Seep Temperature, Activity and Temporal Representation

Most naturally occurring asphalt seeps are episodic and ephemeral in nature (Kvenvolden & Cooper, 2003). Atmospheric temperature, molecular chain length and composition, gas content, and weathering of asphalt over time can impact the viscosity and flow of natural seeps beyond the underlying geology and tectonic activity making each site unique (Hein, 2017; Marcon et al., 2018; Wilson et al., 1974). This impacts the capacity of the seep to entrap and preserve floral and faunal material. Generally, however, increasing temperatures are observed to decrease asphalt viscosity allowing for increased flow (Puttagunata et al., 1993). Casual observations of seeps at the La Brea Tar Pits indicate an ambient threshold of approximately 18° C before seeps viscosity and flow appears liquid or ‘sticky’ enough for entrapment (Holden et al. 2013).

Extreme maximum temperatures recorded by the seep subsurface temperature loggers (Figure 2-2) can be explained by the lower albedo and higher heat retention of asphalt (Golden & Kaloush 2006). Temperature patterns match research on the response of asphalt roads to temperature change including an expected increased amplitude of daily temperature change in the warmer months and decreased amplitude in cooler months, along with far more variable maximum daily values than minimum daily values (Herb et al. 2009).

Seep temperature data suggests that on hot days smaller animals caught in seeps might not have just struggled with a sticky trap, but also may have dealt with debilitating or lethally high temperatures. Studies on small placental mammals have found that upper critical thermal limits, temperatures at which individual organisms can only exist for short periods of time without risking injury and eventually death from heat stress (Telemeco et al. 2017), are reached at body temperatures of 42 to 45 °C (Erskine & Hutchison 1982; Riek & Geiser 2013) which can be brought about with exposure to temperatures of ~39.5°C in as little as 4 hours when deprived of food and water (Leon et al. 2005). Without the ability to replenish water or to rely on behavioral adjustments to protect from heat, animals trapped in the asphalt seeps would be especially vulnerable to heat stroke. Maximum daily temperatures reached during the majority of the year would be enough to put smaller bodied birds, lizards, and mammals at extreme risk (Whitfield et al. 2015; Telemeco et al. 2017).

The timing of fruiting for the species identified in both the exposed and stream seep surface samples is primarily limited to warmer months, corresponding to average seep temperature rising above 18° C. This suggests that asphalt seep assemblages may by biased towards species with particular phenology, namely those species that fruit in the warmer times of the year. While cooler temperatures at night may temporarily prevent submersion of plant material, as long as average temperatures are warm enough, material that falls on seeps during cooler times of day could still become trapped during late morning and afternoon periods as temperature, asphalt viscosity, and seep flow increases. This hypothesized phenological bias is supported by the absence of trapped material from species recorded in the 10 meter transects that have fruiting times in the late fall, winter, or early spring (Figures 2-4 and 2-5).

Seep Spatial Representation

The species makeup of the surface samples from the exposed and stream seeps had no overlapping species (Jaccard similarity of 0). Both samples were dominated by species located within 5 meters of the seep, with 77-91% of plant material coming from species found within this zone. These included *C. melitensis*, *S. leucophylla,* and *D. spicata* for the exposed seep, and *P. monspeliensis*, *H. squarrosa*, *Eriogonum fasciculatum*, and *B. salicifolia* for the stream seep. Species present in the seep, that were not in the 10-meter surrounding transects, included *P. racemosa* in the exposed seep, and *Sonchus* sp. and *Q. agrifolia* in the stream seep. In both cases, these species were observed in proximity growing at higher elevations in the canyon above the monitored seeps and were likely transported by wind. An exception here is the elderberry seed (*S. nigra* ssp. *caerulea*) found in the exposed seep. While *S. nigra* ssp. *caerulea* is not uncommon in the surrounding range, it was not observed in the general area of the seep. The nearest observation on the Calflora database is approximately 5 km to the South. The fruits of *S. nigra* are an important food source for many Passeriformes like the California Towhee (*Melozone crissalis*) which was captured on camera near the stream seep (Figure 2-3C), making transport by animal a likely means of deposition of this material into the seep. Introduction of extra-local plant material to a hydrocarbon seep via animal fecal matter or entrapment and decomposition of the animal itself has been recognized in previous studies. Mychajliw et al.

(2020) recently identified preserved woodrat coprolites containing plant matter at LBTP. Plant material from a deposit containing giant ground sloths in Ecuador was found to be consistent with digested fodder and thought to represent sloth stomach contents or coprolites (Lindsey et al. 2020). And, the presence of such material has been suggested at two other asphaltic localities in Ecuador and Peru (Churcher, 1966). The increased presence of plant species that include animals as a mechanism of seed dispersal along with the increased faunal material in the exposed seep sample suggests at least some of the exposed seep remains may have gotten there via fecal matter or trapped fauna.

The seasonality and volume of high energy water flow during colder periods suggests species occurring outside the surveyed zone were more likely transported by wind or animals, as seeds transported during the wet season would have had limited opportunity to be deposited in or near the seep. Wet periods also coincided with the transport and deposition of large volumes of sediment over the stream seep visible in Figure 2-2, creating another barrier for plant material to become trapped as more time elapses for asphalt to once again reach the surface. Some plant material may be deposited with the sediment and later preserved as asphalt resumes it’s flow upward, however the higher energy context of deposition may sort lighter plant material out. The cooler temperatures of the stream seep compared to the exposed seep were likely the result of its proximity to water and its shaded position.

The natural variations in activity between seeps beyond temperature seasonality likely encourages further differences in taxa represented. Overall, the stream seep captured seeds of smaller mass while the exposed seep captured seeds with greater mass (although an unpaired two-samples Wilcoxen test for non-parametric samples does not show the differences as statistically significant; Figure 2-6). This trend supports a relationship between seep activity, temperature, and mass of material captured. The reduced viscosity of the stream seep may have played a role in the increased presence of smaller, lighter, wind-dispersed plant material. Seep contents from this study suggests that seep assemblages are highly localized and generally limited to the taxa growing in the immediate vicinity.

While there were taxa growing within the surveyed region around the seeps that produced fruit in cooler seasons, like *A. californica*, *A. douglasiana*, *B. maritima*, and *Salix* sp., none of them had any presence in seep surface samples. Surface samples were limited to taxa that fruited year-round, or just in summer and early fall, the warmest months. This absence of taxa with cooler-season fruiting periods from the surface samples, despite their proximity to the seep, strongly suggests that processes beyond spatial patterns play a role in seep sample representation. This leaves seasonal changes in seep activity and viscosity as the most likely explanation for the observed bias in plant material.

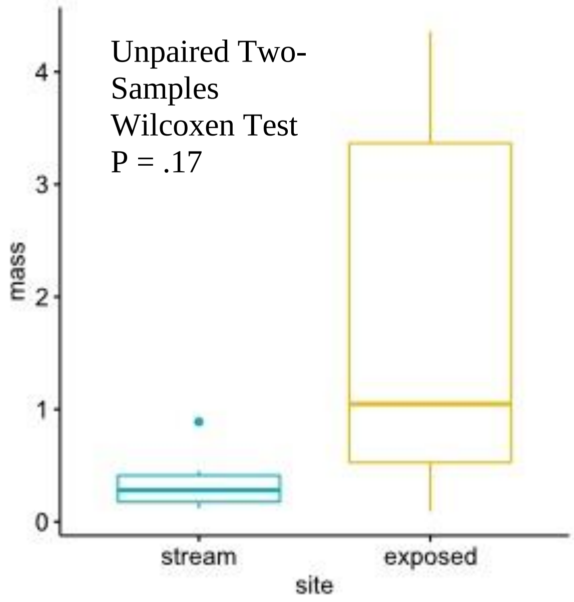

Figure 2-6: Box plot diagram of measurements of seed mass between stream and exposed site surface samples. Unpaired two-samples Wilcoxen test of the two groups produced a P value of .17

2.5 Conclusion

In summary, hydrocarbon seep fossil plant assemblages appear to be highly localized and are less likely to be transported by water than by wind. However, introduction by fauna, including extra-local transport, is likely an active process in seep plant assemblage formation.

There also appears to be a strong seasonal bias towards plants that produce fruit in late summer and early fall when average temperatures are at their warmest and seeps most viscous. Additionally, factors like temperature and seep flow may bias deposits based on seed mass, with less actively flowing seeps trapping smaller lighter material. Insight into how, when, and why plant material is deposited into hydrocarbon seeps, gives us a better idea of spatial representation of seep assemblages and what might be missing, allowing for a more nuanced picture of climates and ecologies in the past at LBTP and terrestrial asphaltic fossil deposits that exist across the globe (Wilson et al. 1974; Mychajliw et al. 2020).

2.6 References

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Chapter 3 Identification of Fossil Juniper Seeds Preserved in La Brea Asphaltum Deposits: Implications for Climate Change and Drought in the Late Pleistocene

3.1 Abstract

The late Quaternary plant macrofossils of the La Brea Tar Pits (LBTP) in Los Angeles, California, USA offer an exceptional opportunity to examine long-term, local scale vegetation dynamics with high taxonomic resolution across a variety of climatic and environmental shifts spanning the past 55,000 years. This study uses a multi-method analytic approach to identify species of *Juniperus* seeds recovered at LBTP and provide new insights into the vegetation and climatic history of the site. Although abundant in the late Pleistocene fossil record, junipers are not recorded from the modern native flora of the vicinity. Fluorescence microscopy, 2D image analysis, computed tomography (CT) scans, species distribution modeling (SDM), and radiocarbon dating are used to resolve the species of *Juniperus* at the site. Methods are used to diagnose a previously unidentified small-seeded juniper that is commonly preserved in the LBTP asphalt deposits and place it in a chronological context. 2D image analysis and SDMs identify the most likely species as *Juniperus* cf. *scopulorum* (Rocky Mountain juniper). The small-seeded juniper of La Brea represents the most pronounced example of plant range extension and eventual extirpation from the Ice Age flora at LBTP. Comparisons of radiocarbon dates between fossil *Juniperus californica* (California juniper) and *J.* cf. *scopulorum* reveal a reciprocal relationship in the presence of *J.* cf. *scopulorum* and *J. californica* during the late Pleistocene prior to the local extinction of both species at the site by the start of the Holocene. Climate modeling based on modern ecoclimatic relationships for *Juniperus* species suggest strong influences from insolation seasonality that may not have been visible through less taxonomically

precise proxies and two possible periods of extended drought at ~48-44.5 ka and ~29.3-25.2 ka. The cause of the local extinction of both junipers at LBTP by ~12.3 ka may reflect combined forces of climate and changing fauna, increasing fire frequency and largely making the Holocene Los Angeles Basin uninhabitable for this taxon.

3.2 Introduction

The combined use of paleoecological data and paleoclimate reconstructions, in recent decades, has provided exciting new avenues of research in the quest to better understand the dynamic interplay between biogeographic processes and climate (Harbert & Nixon, 2018; MacDonald et al., 2008; Willis & MacDonald, 2011). However, the strength of this research is strongly influenced by the number and variety of paleoecological data sources made publicly available (MacDonald et al., 2008). Plant macrofossils, fossils that can be seen with the naked eye and identified using low-magnification microscopy, offer rare opportunities to understand past vegetation change on a species-level (Follieri, 2010; Jackson et al., 1997; Jackson & Weng, 1999). They can give better insight into processes controlling range dynamics, species resilience and turnover on a local-scale. However, compared to other fossil indicators of vegetation, such as palynomorphs, plant macrofossils are relatively rare and often only capture limited or discontinuous slices of time.

The asphaltic fossil deposits at the La Brea Tar Pits (LBTP) are noteworthy in that they have preserved abundant and diverse plant macrofossils, including seeds, leaves, and wood, over the site's ~60 ka depositional history. The site, a world-renowned Ice Age fossil locality in Los Angeles, California, on the traditional, ancestral and unceded territory of the Gabrielino/Tongva peoples (figure 3-1), is well known for Ice Age megafauna (large mammals such as sabertoothed cats, dire wolves, and mammoths). Very little attention has been paid to the abundant plant material preserved in LBTP's asphalt deposits. The botany of LBTP has been the focus of surprisingly few publications to the detriment of a broader understanding of ecological and climate shifts in the Los Angeles Basin and coastal Southern California (Stock, 1992; Frost, 1927; Gerhart et al., 2012; Templeton, 1964; Ward et al., 2005; Warter, 1976, 1979).

The expansive timeframe captured by LBTP's active hydrocarbon seeps provides an exceptional opportunity for long-term reconstructions of vegetation with high taxonomic resolution across the climatically active Late Pleistocene and relatively stable Holocene. This interval, covering marine isotope stages (MISs) 3-1, saw long-term global shifts in climate with the growth and decline of continental glaciers, millennial-scale climate events, and sweeping changes to global ecology with the arrival of humans and the disappearance of much of the world's megafauna (Barnosky et al., 2011). LBTP plant fossils offer a rare opportunity to see how vegetation on the species level responds to environmental shifts on a local-scale.

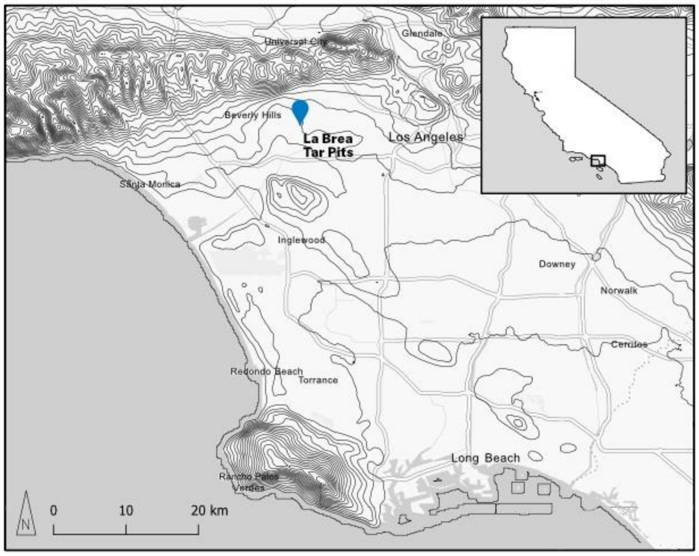

Figure 3-1: Map of the location of the La Brea Tar Pit fossil deposits within the Los Angeles Basin.

While the 130 asphaltic deposits at LBTP were active at distinct periods, many were accumulating and preserving plant and animal remains for thousands of years at a time. This overlapping chronology, as well as the lack of stratigraphy in the asphalt deposits makes associating discrete fossil elements nearly impossible. Radiocarbon dating individual specimens is necessary to place species into chronological context (Friscia et al., 2008; Holden et al., 2017). An accurate reconstruction of past vegetation using AMS radiocarbon dated plant macrofossils at LBTP can potentially reveal more subtle patterns of local climatic and ecological change than more common palynological proxies (Jackson et al. 1997) and yield valuable information on future challenges to the flora of California (Barnosky et al., 2017).

This study uses a multi-method approach to identify one of the most common plant macrofossils found at LBTP, a small-seeded *Juniperus,* which has yet to be identified to the species level. Today, *Juniperus* is not recorded as a native genus growing in the vicinity of the LBTP. Scattered California juniper (*Juniperus californica*), another fossil species, are reported in mountainous areas and rocky washes approximately 20 km distant from the LBTP (*Calflora*, 2022). The LBTP collections house well over 550 specimens of juniper seeds of *Juniperus californica* and an unidentified small-seeded juniper.

We use 2D Digital image analysis and 3D computed tomography (CT) model measurements, in combination with fluorescent leaf and branchlet imagery of fossil and modern junipers to identify the small-seeded *Juniperus* fossils to species. We compare these data to eco-climatically hindcasted species distribution models (SDMs) for the Last Glacial Maximum (LGM) for morphologically similar *Juniperus* species to further refine identifications by identifying potential modern counterparts of the LBTP junipers from the perspective of modern climate envelopes. We radiocarbon dated individual identified juniper seed fossils to create a timeline of juniper species presence at LBTP.

3.3 Importance of Species-Level Identification of Juniper

Juniperus is a geographically widespread genus (Adams, 2014). Leaves and seeds of juniper are commonly found preserved in packrat middens, the most common source for plant macrofossils from the southwestern United States from the past 50,000 years. These fossil remains can be important ecological and environmental indicators (Betancourt et al., 2001, 2021; Holmgren et al., 2006, 2010; Inman et al., 2018) as juniper populations are sensitive to changes in temperature, winter precipitation and fire. At the landscape scale, juniper is a keystone taxon in woodlands and their presence influences hydrology, nitrogen cycling (Miller & Wigand, 1994a), day time and night time land surface temperatures (Wang et al., 2021).

Recent decades have witnessed dramatic changes to juniper populations globally, from encroachment of invasive plants (R. B. Jackson et al., 2002; Mueller et al., 2005; Wang et al., 2021; Willson et al., 2008b), slowed recruitment and dramatic die off (Breshears et al., 2005; Fisher, 1997; Kannenberg et al., 2021; Lloret & García, 2016; Lu et al., 2019). *Juniperus* as a genus is considered drought tolerant, as many species demonstrate substantial resistance to water-stress-induced xylem cavitation (Maherali et al., 2004; Willson et al., 2008b). For instance, during successive periods of drought in piñon-juniper woodlands from 1994-2004, pine species were far more susceptible to die off than juniper (Mueller et al., 2005). This is likely due to the vascular structure of juniper that is highly resistant to branch cavitation along with the ability of juniper leaves to withstand negative water potential (Linton et al., 1998). Yet, despite juniper’s ability to tolerate drought, significant mortality of Utah juniper (*Juniperus osteosperma*) is occurring today in the American Southwest due to extreme drought coupled with increased summer and annual temperatures (MacDonald, 2010; Kannenberg et al., 2021).

This juniper mortality is occurring at the lower elevations of Utah juniper's current geographical range (<2000m). This same pattern has occurred in the lowlands of Southern California repeatedly throughout glacial/deglacial cycles of the Late Quaternary. For instance, a severe decline in *Juniperus* spp. pollen in the Late Pleistocene record from Lake Elsinore (LE) (Heusser et al., 2015) occurred during a period of "megadrought" during MIS3 (27.5-25.5 ka). This juniper decline has been attributed to increased air temperatures that accompanied a protracted drought. Following this event, juniper recovered and dominated the Lake Elsinore basin during cooler periods until onset of Bølling Allerød warming at 14.7 ka at which time juniper was nearly extirpated from the record by 13ka. This Bølling Allerød juniper decline is also noted at Owens Lake (Mensing, 2001), Mono Lake (Davis, 1999; Woolfenden, 2003) and in the Santa Barbara Basin (Heusser, 1995; 1998). However, a rise in juniper has been noted in Southern California during colder drier glacial periods in several studies (Heusser, 1998; Heusser et al., 2015; Koehler et al., 2005; McGann, 2015). Therefore, the genus of *Juniperus* may serve as an indicator of dry and cool vs. dry and hot periods based on its abundance in the fossil record.

While a single genus may share physiological attributes that more broadly influence persistence or decline in a given environmental condition, *Juniperus* demonstrates a fair amount of species-to-species variety in environmental response (Lyford et al., 2003; Miller & Wigand, 1994a). The identification of *Juniperus* to species, is necessary to understand the nature of environmental changes taking place (Dimitri et al., 2017; Schupp et al., 1997). Much of the past identification of fossil juniper remains, primarily from packrat middens, has focused on the identification of *Juniperus* leaf scales (Betancourt et al., 2001, 2021; Holmgren et al., 2006, 2010). Because juniper seeds are highly lignified and abundantly produced, they are more likely to preserve in fossil archives—as is certainly the case at the LBTP.

3.4 Methods

3.4.1 Potential Juniper Species Present at LBTP

Templeton (1964) identified two species of juniper from Rancho La Brea: a large-seeded juniper that was assigned to *Juniperus californica;* and a small-seeded juniper which was newly described as an extinct species, *Juniperus hanseni* n. sp. Templeton's new species descriptions were based mostly on seed size and a qualitative characters of resin pit placement from species with cones containing one or two seeds. Templeton's new species description was never published, and occurrences of this taxon are only noted at Rancho La Brea. Given that only one plant species extinction has been documented from the Late Quaternary (Jackson & Weng, 1999), it is more likely that the small-seeded juniper of La Brea is from an extant juniper species now extirpated from Southern California. Here, we use a variety of comparative methods to identify the small-seeded juniper from La Brea. We compare seeds of the small-seeded juniper to those of three extant taxa (*Juniperus virginiana* var *silicicola*, *Juniperus blancoi,* and *Juniperus scopulorum*). These taxa all belong to the *virginiana* group of the *Sabina* sect (Adams, 1983; Adams et al., 1981) and were chosen for comparison because they are multi-seeded junipers with entire leaf margins. Based on foliar material also preserved at LBTP, leaf margins of the small-seeded juniper are also entire (figure 3-2).

Additionally, measurements of leaf scale lengths of these specimens are consistent with recorded lengths of *J. blancoi, J. scopulorum, and J. virginiana.* Measurements of branchlet width at the widest point are representative of only *J. virginiana* and *J. scopulorum*

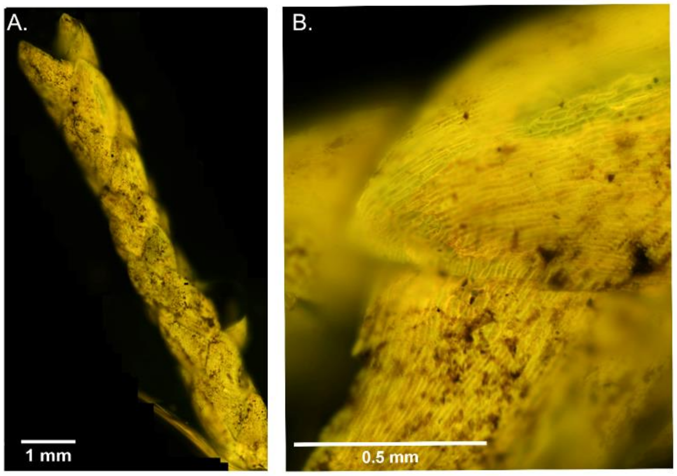

Figure 3-2: (A,B) Fluorescent microscope imagery of fossil branchlet (1469B). (B) close-up of leaf scale with smooth leaf margins and acute-slightly obtuse apical shape.

(Eckenwalder, 2009). Apices of scale leaves range from acute to slightly obtuse aligning with *J. scopulorum, J. virginiana*, and *J. maritima* (Adams, 2014; Farjon, 2017). Branchlet and leaf scale morphological traits most consistently align with those of modern *J. scopulorum* and *J. virginiana*. Seed cone size can also be an important identifying factor of juniper species; however, few specimens show preservation of the original cone, and those that do are highly degraded and don't preserve size or shape.

Templeton (1964) noted that *J. hanseni* n. sp. was most similar to *J. barbadensis,* a native to the Caribbean with a highly restricted geographical range. Adams (2014) synonymized *J. barbadensis* with the more widespread species *Juniperus virginiana* var. *silicicola*, a native of the southeastern Atlantic coast of the USA. We follow the taxonomy of Adams and use specimens of *J. virginiana* var. *silicicola* as modern comparative material in this study.

No members of the *virginiana* group currently occur in California. However, two packrat middens located within Owens Valley, California dated to 21,434 cal BP (17680 ^{14}C years) (Koehler & Anderson, 1994) and 12,156 BP (10330 ^{14}C years) (Wigand, 2002) contain fossils identified as *J. scopulorum*. Additionally, two out of three beetle species identified as possible creators of beetle galleries in wood recovered at LBTP, *Phloeosinus hoferi* and *P. keeni,* are only known to use *J. scopulorum* as a host (Holden & Harris, 2013a). Fossil leaf morphology and LBTP beetle galleries, suggest *J. scopulorum* as a primary candidate for the small-seeded fossil juniper. For the sake of thoroughness, J. *virginiana* and *J. blancoi* are also considered in the seed-analytic work employed in this study due to their morphological similarities to *J. scopulorum*. Today, the nearest populations of *J. scopulorum* are in Nevada.

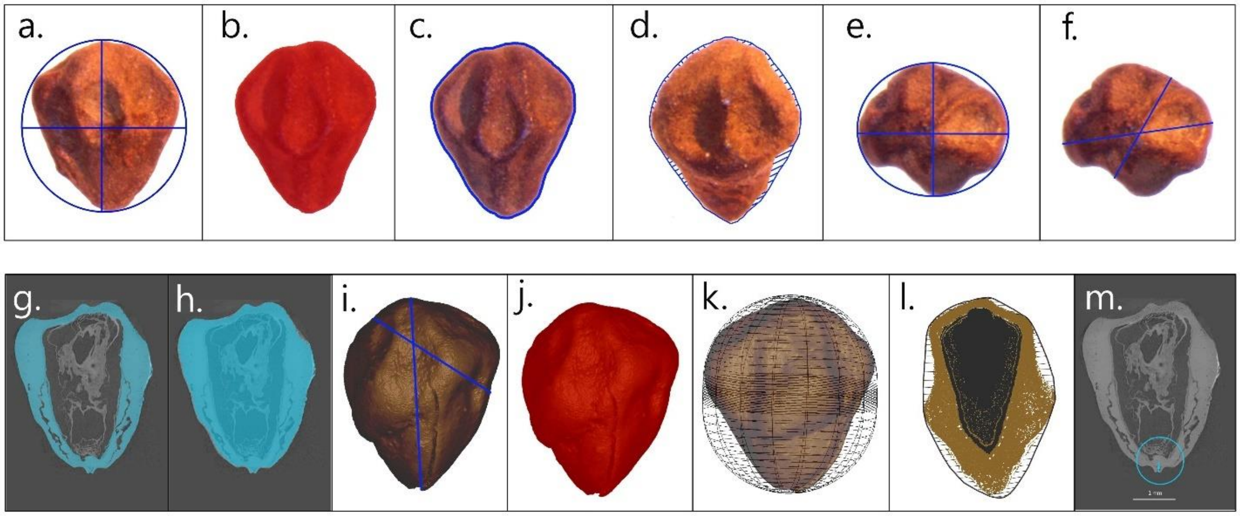

Figure 3-3: Illustration of morphological measurements used to analyze seeds (a-f): 2D image analysis a) major and minor axis of best fit ellipse/roundness b) area c) perimeter d) solidity e) aspect ratio of basal perspective f) Feret's minimum and maximum diameter (g-m) CT scan measurements g) integument volume h) total volume of seed i) mean Feret diameter from measurements with 5° perspective shifts j) surface area k) ratio of empty space within the closest fitting capsule to seed volume l) ratio of empty space within a convex hull to seed volume m) length and width of the seed micropyle.

3.4.2 2D Image Analysis

Fossil and modern juniper seeds (n=143 total) were photographed with the same lateral and basal perspective (figure 3-1) under a stereoscopic microscope and analyzed with the open-source digital image analysis software "ImageJ" (Schneider et al., 2012). Modern *Juniperus virginiana* seeds (n=64), modern *Juniperus blancoi* (n=10), *Juniperus scopulorum* (n=53), and fossil *Juniperus* seeds of the small-seeded variety (n=17) were imaged for analysis. Seeds used for imaging were sourced from The California Botanic Garden's Seed Conservation Program seed bank, LBTP modern botanical reference collection, and LBTP fossil collection. Lateral area of seed in square mm, major and minor axis of the best fit ellipse, roundness, solidity (being the ratio of space not occupied within a convex hull surrounding the seed), basal ratio of Feret's minimum and maximum diameter, and basal aspect ratio were measured and calculated (figure 3-3). The data structure of the specimen measurements was examined using Principal Component Analysis (PCA) biplots to better understand relationships between seed measurements and species divisions.

3.4.3 CT Scans of Seeds

In addition to 2D imagery, specimens of modern *J. virginiana* (n=10), *J. blancoi* (n=5), *J. scopulorum* (n=5), and the small-seeded fossil *Juniperus* (n=5) were CT scanned to obtain volumetric data and measurements of interior structures. Seeds were scanned at the University of Texas High-Resolution X-ray CT Facility with a Zeiss Flat panel, 70kV, 8.5W at a voxel size of 5.5 microns. Overall volume of seeds was measured, as well as interior and integument volume, ratio of empty space within the closest fitting capsule to seed volume to compare distribution of seed mass, ratio of empty space within a convex hull to seed volume to compare pitting on the exterior of the seed integument, length and width of the seed micropyle and the ratio between, Feret diameters, and surface size (figure 3-3). Like the 2D imagery, the data structure of the measurements was examined using Principal Component Analysis (PCA) biplots to better understand relationships between volumetric data and species divisions.

3.4.4 Principal Component Analysis

Principle component analysis (PCA) , a quantitative exploration of measurement contributions to species differentiation (Chen & Manchester, 2007; Lever et al., 2017), was carried out on select measurements of both 2D images and 3D CT scans. The PCA was conducted using the FactoMineR multivariate analysis package in the open-source software R and R Studio. No scalings were performed on seed data prior to analysis. The first two unrotated principal components of those analyses are presented in the paper as they represent the majority of variance in the data.

3.4.1 Radiocarbon Dating

Fossil deposits at LBTP exhibit post-depositional movement and mixing of fossil material (Friscia et al., 2008) making dating by association or stratigraphic layer unreliable (Holden & Southon, 2016). Fossils must then be individually radiocarbon dated to be placed into a chronological context with any degree of certainty. Small-seeded fossil *Juniperus* seeds (n= 34) and *Juniperus californica* fossil juniper seeds (n= 22) were each dated individually by AMS radiocarbon dating to establish periods of presence at LBTP. Samples were processed and run at the Keck Carbon Cycle AMS Laboratory at University of California, Irvine.

La Brea fossil material is preserved by asphalt that can bias sample dates, making them appear older. To avoid this, specimens were sonicated in a 2:1 toluene:methanol solution (following Fuller et al., 2015), followed with an acid-base-acid wash with 1N HCL and 1 N NaOH, and bleached to holocellulose using a 1:1 mixture of 1 N HCl and 1 M NaClO2 (following Mychajliw et al., 2020) to ensure no contamination by asphalt.

Dates are calibrated with the IntCal20 calibration curve (Reimer et al., 2020) by OxCal v4.4.4 (Bronk Ramsey, 2021) as individual distribution curves and mean date distribution points (Bronk Ramsey, 2009). Estimates of extinction period (or extirpation in LBTP's case) for *J. californica*. and the small-seeded juniper are calculated using the Guassian-resampled inverse-weighted McInerny (GRIWM) approach as described in Bradshaw et al. (2012) and Saltré et al. (2015) as a method for overcoming sampling bias in taphonomic processes and fossil recovery for establishing the disappearance point of a given species. The assumption being that final fossil radiocarbon dates will lie earlier than the point of species' actual disappearance. Through a down weighted interval procedure to account for the changing frequency of fossil preservation accompanying changing abundance of species through time and treatment of uncertainties the GRIWM approach has been found to be highly accurate and estimating the period of true disappearance (Saltré et al., 2015; Villavicencio et al., 2016).

3.4.2 Species Distribution Models

SDMs describe the relationship between species occurrences and the environmental conditions at those locations. Hindcasts of species paleodistributions can be produced by developing models using contemporary species data and climate predictors, then projecting those models to paleoclimate conditions (Franklin et al., 2015). While substitutions of space for time intrinsic to hindcasting or forecasting SDMs can yield imperfect results based on the limitations of realized niche space (Blois et al., 2013; Veloz et al., 2012), SDMs can be a powerful tool for investigating past changes in paleobiology (Blois et al., 2013; Franklin et al., 2015; Maguire et al., 2015; Svenning et al., 2011). In the case of this study, they can serve to better illuminate what species presences are most likely, based on present distributions. We used Maxent, a correlative modeling method, to estimate the past distributions of five juniper species (*J. blancoi,* *J. californica*, *J. maritima*, *J. scopulorum*, and *J. virginiana*) based on estimated climate during the Last Glacial Maximum. The Maxent logistic output is a continuous grid of values from 0 to 1, and can be interpreted as a ranking of sites by habitat suitability (Elith et al., 2011). Maxent performs well with small sample sizes (Anderson & Gonzalez, 2011; Wisz et al., 2008) and has shown greater transferability than several other modeling methods (Heikkinen et al., 2012).

Nineteen contemporary bioclimatic variables were acquired from WorldClim version 2.1 (Fick & Hijmans, 2017), which is available at approximately 1-kilometer spatial resolution. Variables were clipped to the North American continent, excluding Hawaii, the Great Lakes, and the Arctic Cordillera (1.0) and Tundra (2.0) Level I Ecoregions (U.S. Environmental Protection Agency 2010). In order to identify and remove highly collinear continuous variables ($|r|> 0.8$), correlation analysis was performed using the raster.cor.matrix() function in the R package ENMTools. Comparisons between paleoclimate models found reconstructed precipitation to be the most variable and least reliable (Braconnot et al., 2012), for this reason, we drew primarily from temperature based environmental layers. The six variables ultimately included in modeling were annual mean temperature, minimum temperature of the coldest month, mean temperature of the warmest quarter, mean temperature of the wettest quarter, annual precipitation, and precipitation of the warmest quarter. The same bioclimatic variables were acquired from the ecoClimate Project’s (Lima-Ribeiro, 2015) Community Climate System Model version 3 (CCSM3) layers to simulate climate over the last 21,000 years.

Presence data for each species were acquired through the Global Biodiversity Information Facility (GBIF 2022a-e). In lieu of true absences, Maxent contrasts presence records with pseudo-absences randomly drawn from the model background. Because biased sampling data or large spatial extents can result in overfitted models and/or inflated performance statistics

(Phillips et al., 2009; VanDerWal et al., 2009), it is recommended that pseudo-absences be preferentially selected from more densely sampled areas (Elith et al., 2011; Merow et al., 2013). We estimated sampling density for each species using the kde2d() function in the R package MASS, which produced a kernel density estimate based on species presences. Density values were normalized from 1 to 100 using a linear function, and cells within 10-kilometers of a presence record were excluded from the grid.

Modeling was performed in Maxent version 3.4.4 using auto-feature settings. Duplicate presence records, i.e. multiple points occurring in a single model grid cell, were removed and 10,000 background (pseudo-absence) points were selected using each species' bias grid. We explored several regularization multipliers (0.5, 1.0, 1.5, 2.0) in order to identify a value that maximized model fit on cross-validated datasets (Merow et al., 2013; Radosavljevic & Anderson, 2014). We employed a spatial form of four-fold cross-validation in which the folds are determined by latitude and longitude, similar to the "block" partitioning method in the R package ENMTools, which is preferred for studies where non-analog conditions are possible (e.g. when transferring models across time) (Kass et al., 2021; Muscarella et al., 2014). The Grouping Analysis tool in ArcMap 7.1 was used to initially split species records into 4 bins, then made minor manual adjustments to balance bin sizes as much as possible. In each model run, three bins were used for model training and the fourth was withheld for testing. Cross-validated models were evaluated using three metrics as in Muscarella et al., 2014: 1) test area under the receiver operating curve (AUC_{Test}), a discriminatory measure of a model's ability to distinguish testing samples (withheld from model training) from pseudo-absences, 2) the difference between the AUC of model training samples and AUC_{Test} (AUC_{Diff}), and 3) minimum training presence (MTP) test omission rate, i.e. the percentage of test samples that fall below the MTP threshold, which is equal to the lowest predicted value of a training sample. $\mathrm{AUC}_{\mathrm{Diff}}$ and MTP omission rate quantify model overfitting; high values are expected for overfitted models (Warren & Seifert, 2011). We chose the regularization multiplier that best balanced discrimination and fit (Appendix figure A-1) and verified the selection by a qualitative assessment of prediction maps. LGM paleodistributions were projected from models fitted using this regularization multiplier and all available presence data (Appendix Table A-1).

3.5 Results

3.5.1 2D Image Analysis

The eight measurements included in the analysis explain 73.3% of the variation in the first two axes (figure 3-4). Size measurements such as area and perimeter were identified as the most important variables with variables related to basal circularity closely following. Solidity, which measured the ratio of empty space to seed area within a convex hull (a shape similar to a rubber band wrapped around the exterior of the seed) which gave the best estimation of resin pitting size and presence contributed the least to observed variation in the first two axes (under 5% for both PC1 and PC2). Distinctive clusters of seed species are most apparent in this analysis. Plots of the first two axes demonstrate a fair amount of overlap between regions of fossil juniper and *J. scopulorum* as partially with *J. blancoi.* The fossil juniper doesn't plot as closely to *J. virginiana.* Strong positive loadings of general size variables (major and minor axis, perimeter and area) distinguish the fossil juniper, *J. scopulorum*, and *J. blancoi* from *J. virginiana.* Solidity, our proxy for resin pitting, contributes a smaller amount to that differentiation. Proxies for roundness of lateral and basal perspectives were generally unhelpful in differentiating between *J. virginiana*, *J. scopulorum,* and the fossil juniper, but do appear to have a greater contribution to the differentiation of *J. blancoi* from the rest of the species.

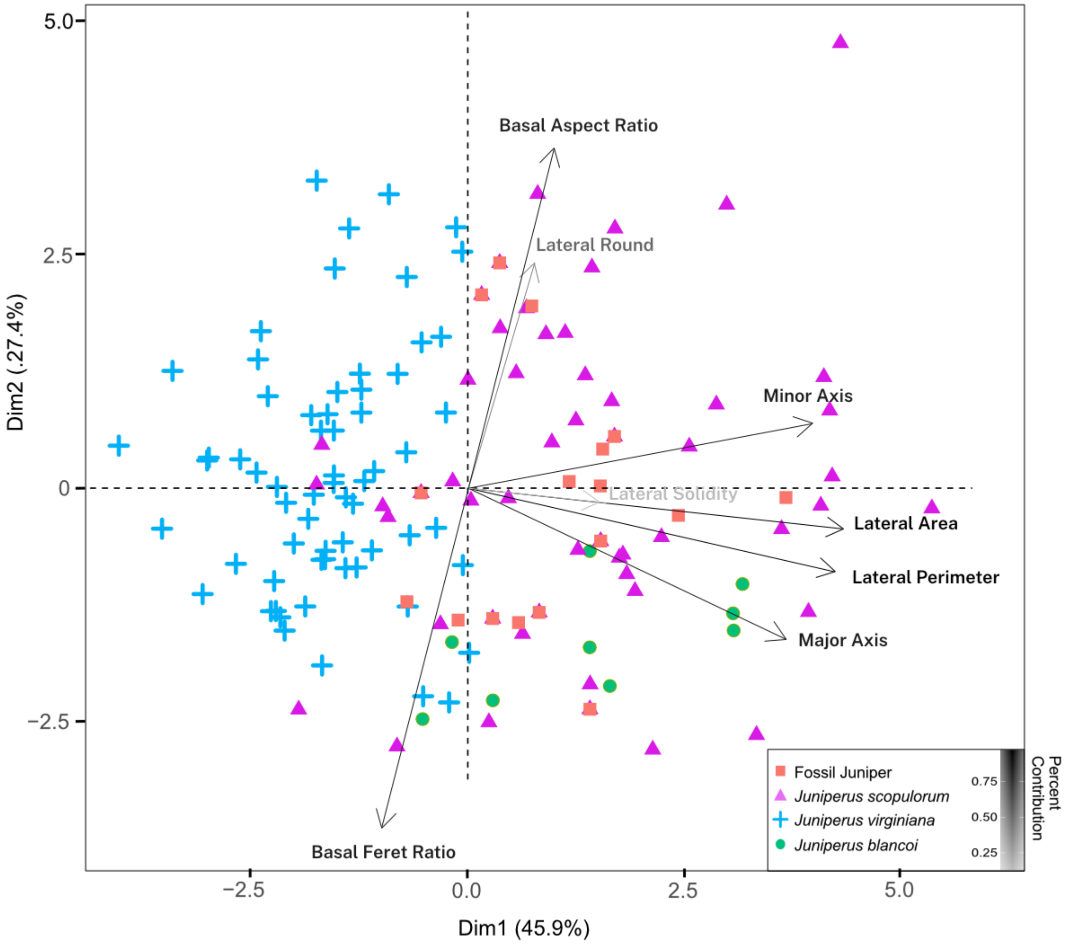

Figure 3-4: PCA biplot of 2D morphological measurements. Fossil juniper is represented by a red square, J. scopulorum by purple triangles, J. virginiana by blue crosses, and J. blancoi by green circles.

3.5.2 CT Scans

The eleven measurements included in the analysis explain 73.3% of the variation in the first two axes (figure 3-5). Size and volumetric measurements explain the majority of variation. The calculated ratio of micropyle length and width followed as next important to variation represented followed by the calculated ratios for empty space within the capsule and convex hull. Clustering between species is less apparent in this analysis. Similar to the 2D data, strong positive loadings of general size variables (volume, integument volume, mean Feret, max Feret, and surface area) contribute the most to differentiations between fossil juniper, *J. scopulorum*, and *J. blancoi* from *J. virginiana.* Again, our proxy for resin pitting (the ratio of negative space in the convex hull) contributes to this differentiation to a smaller degree. Further differentiation between all represented species is seen with the strong positive loading of the variable, micropyle width, and the negative loadings for ratio of micropyle width/length

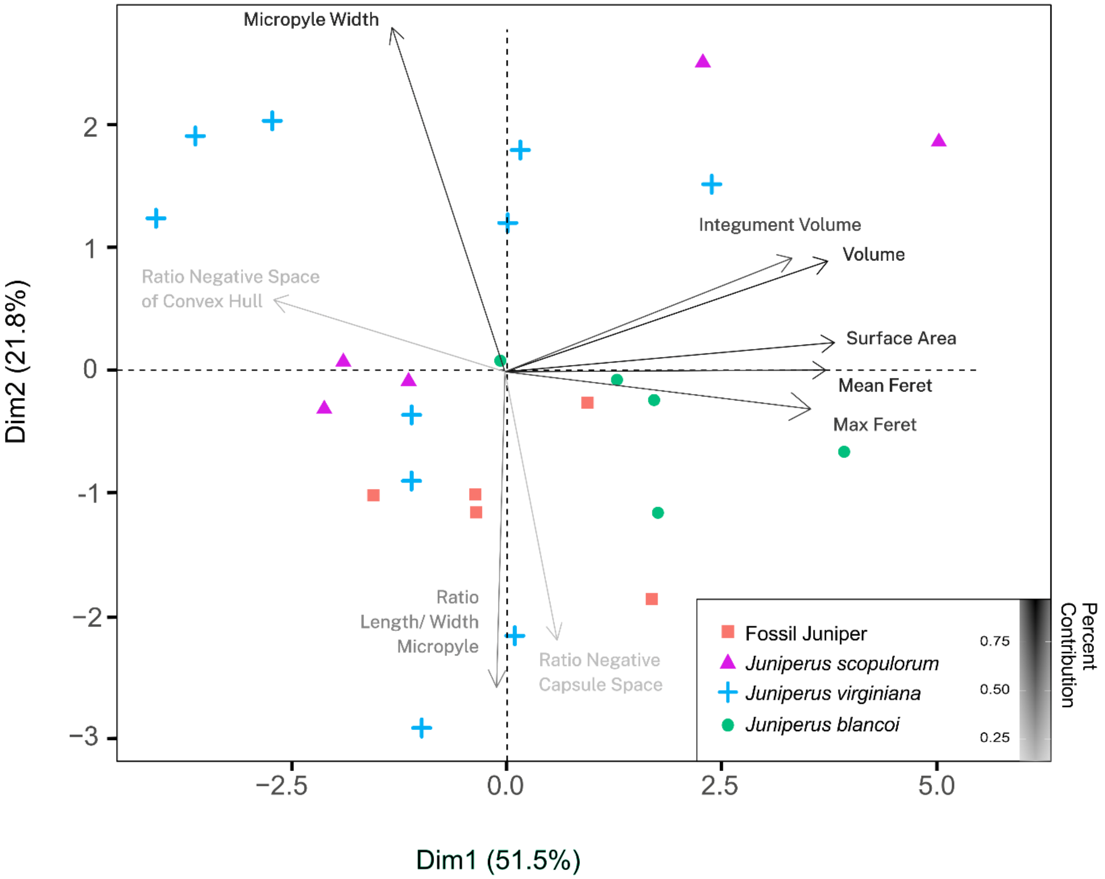

Figure 3-5: PCA biplot of CT morphological measurements. Fossil juniper is represented by a red square, J. scopulorum by purple triangles, J. virginiana by blue crosses, and J. blancoi by red squares.

and negative capsule space. *J. blancoi* and the small fossil juniper show closer alignment in plotting of the CT scan measurements than they do in the PCA for the measurements from 2D imagery, this may be a product of sample size or the added complexity afforded by CT scan analysis. *J. virginiana* remains the least closely aligned species.

3.5.3 Radiocarbon Dating

Direct AMS radiocarbon dates on 34 fossil specimens of the small-seeded juniper type (Appendix Table A-2) indicate an intermittent presence between the beginning of the record at approximately 53 ka (calendar years BP) to the latest fossil occurrence, which has a median calibrated age of 15147 ka. The oldest specimens have probability distributions that extend beyond the range of calibration of IntCal20, their calibrated median ages in this state fall between 53 and 52 ka. Extended time periods where an absence of dated specimens is observed, occur between ~48-44.5 ka and ~29.3-25.2 ka.

Direct AMS radiocarbon dating of *J. californica* specimens also yielded dates on the edge of calibration, mean radiocarbon ages as early as 51800 with an error of 2500 (median calibrated age of 52885) and one date of 57 ka and older. Again, the probability distributions of older dates with errors extend beyond the range of calibration of IntCal20.

Radiocarbon dating of the small fossil juniper in comparison to fossil *J. californica* at LBTP *(Tab. 2 in Supplementary Data)* show temporal occurrences of for the two species. However, as these dates are nearing the limit of the period radiocarbon dating can accurately measure, they must be interpreted with a small amount of skepticism. An initial period of replacement of the small juniper with *J. californica* occurs at ~48-44.5 ka. The most prominent episode of *J. californica* replacing the small juniper occurs at ~29.3-25.2 ka. *J. californica* has ultimate estimated time of local extinction of 25.4-24.2 ka with a median value of 25 ka. The small juniper has an ultimate estimated time of local extinction 13-11.7 ka with a median value of 12.3 ka.

3.5.4 Species Distribution Models

Hindcasted SDMs of juniper for the LGM for both *J. scopulorum* and *J. virginiana* show a movement of climate space southward compared to their modern distributions (figure 3-6). The climate space suitable for *J.* maritima moves south to coastal Washington, Oregon, and northernmost California, with some appropriate climate space appearing along the California/Mexico border. The appropriate climate range of *J. blancoi* focuses further south into Mexico, while pushing coastward in the continental United States and Canada. Like *J. maritima,* it runs coastal in Washington and Oregon, but only just reaches the northernmost coasts of California. *J. scopulorum's* range, is concentrated in the southwestern states of the US and moves prominently into the northern portion of the Mojave Desert. Appropriate coastal areas in California are greatly reduced during the LGM, but some appropriate climate space still exists within the Los Angeles Basin. *J. virginiana's* range, in modern times occupies almost the entirety of the eastern half of the U.S. and is restricted primarily to southeastern states with a small strip of appropriate climate space running centrally along what is likely the Colorado and Little Colorado rivers during the LGM.

3.6 Discussion

3.6.1 Identification of Juniperus species through multi-method analyses

The PCA cluster of the small-seeded fossil juniper aligns most closely to the cluster of *J. scopulorum* based on 2D morphological measurements, indicating similar importance of variable

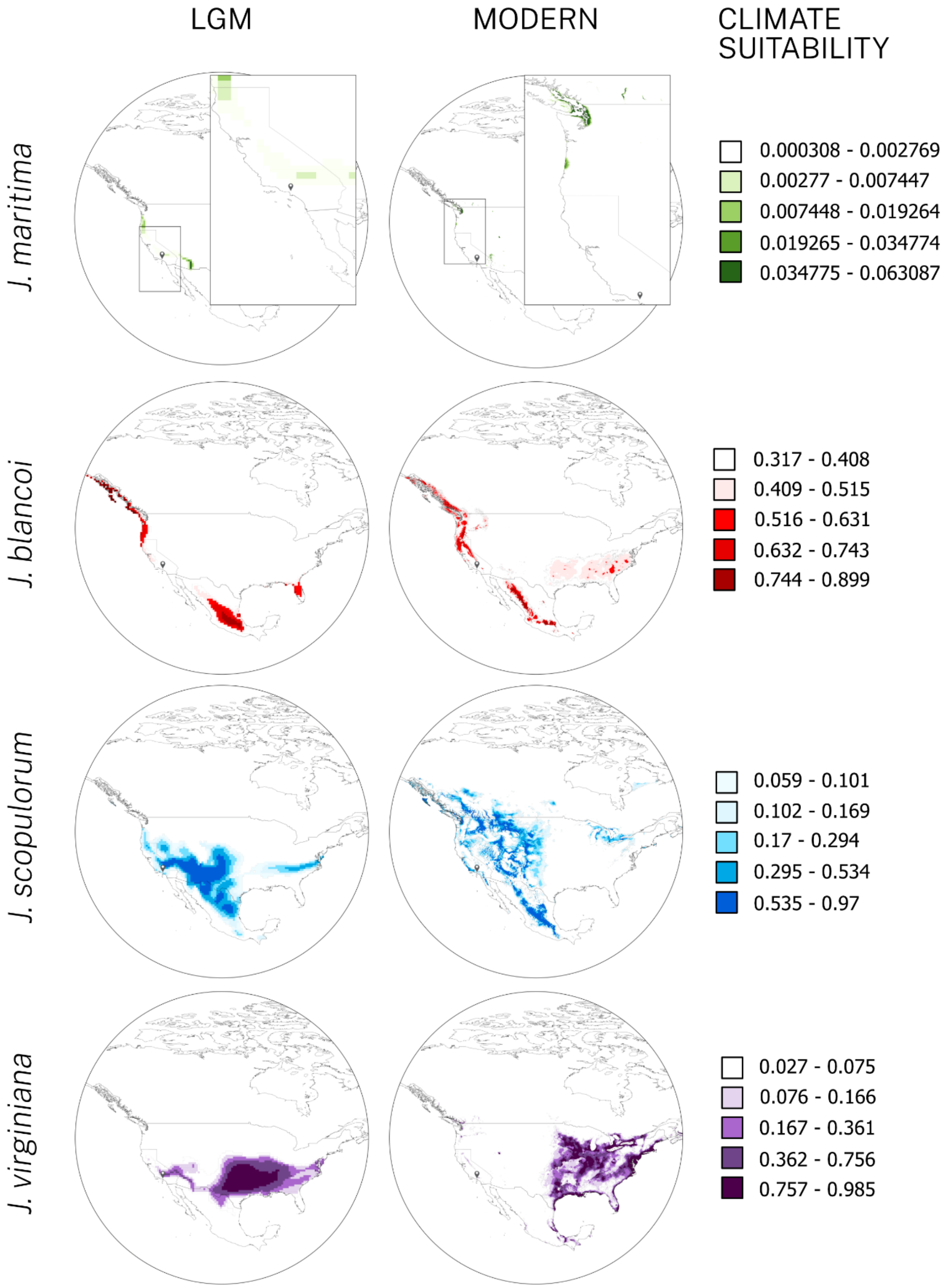

Figure 3-6: Hindcasted LGM and modern species distribution models of candidate juniper species pertaining to seed fossils at La Brea Tar Pits, based on modern GBIF presence data, contemporary bioclimatic variables from WorldClim 2.0, and LGM variables from ecoClimate Project CCSM3 prepackaged layers. LBTP location marked by black marker.

loadings. There is overlap with *J. blancoi,* however the populations of *blancoi* seeds measured do not encapsulate the range of variation represented in the fossil seeds. PCA of CT scan seeds is performed on a relatively small number of specimens compared to the PCA for 2D image analysis (n = 143 versus n = 25) and does not exhibit clustering by species as clearly as the 2D measurements, though some does occur. *J. scopulorum* and *J. blancoi* align most closely to the cluster of fossil juniper compared to *J. virginiana*, however, there is overall, less overlap between species. Overlapping variables between the 2D and CT PCAs, such as size-based measurements and resin pitting proxies, exhibit similar importance and patterns in differentiating clusters. The differences observed in the two analyses may be a product of the differences in sample size or it's possible that the addition of morphological measurements of elements like the micropyle and 3-dimensional resin pitting may allow for more differentiation between groups. CT scanned imagery has potential to be an efficient and robust approach for delineating *Juniperus* species from seed morphology alone with smaller sample sizes than 2D, however, further experimentation is needed.

Results of the hindcasted SDMs reinforce *J. scopulorum* as the most likely modern candidate for the small-seeded fossil *Juniperus* specimens. Hindcasted climate space appropriate to *J. scopulorum* is pushed southward from interior western states east of the Sierra Nevada into the desert and mountain regions of southeastern California and to a lesser degree, the Southern Coastal region. Modern and hindcasted moderate to highly suitable climate space of *J. maritima* and *J. blancoi* does not approach LBTP or coastal Southern California. The hindcasted model for *J. virginiana* climate space does predict moderate to high suitability of climate space in Southeastern California, however *J. virginiana* was the least similar to the fossil juniper seeds in both 2D and CT analysis and has no fossil record in the Southwest. There are fossil presences of *J. scopulorum* in the Owens Valley between the Eastern Sierra Nevada and the White Mountains,

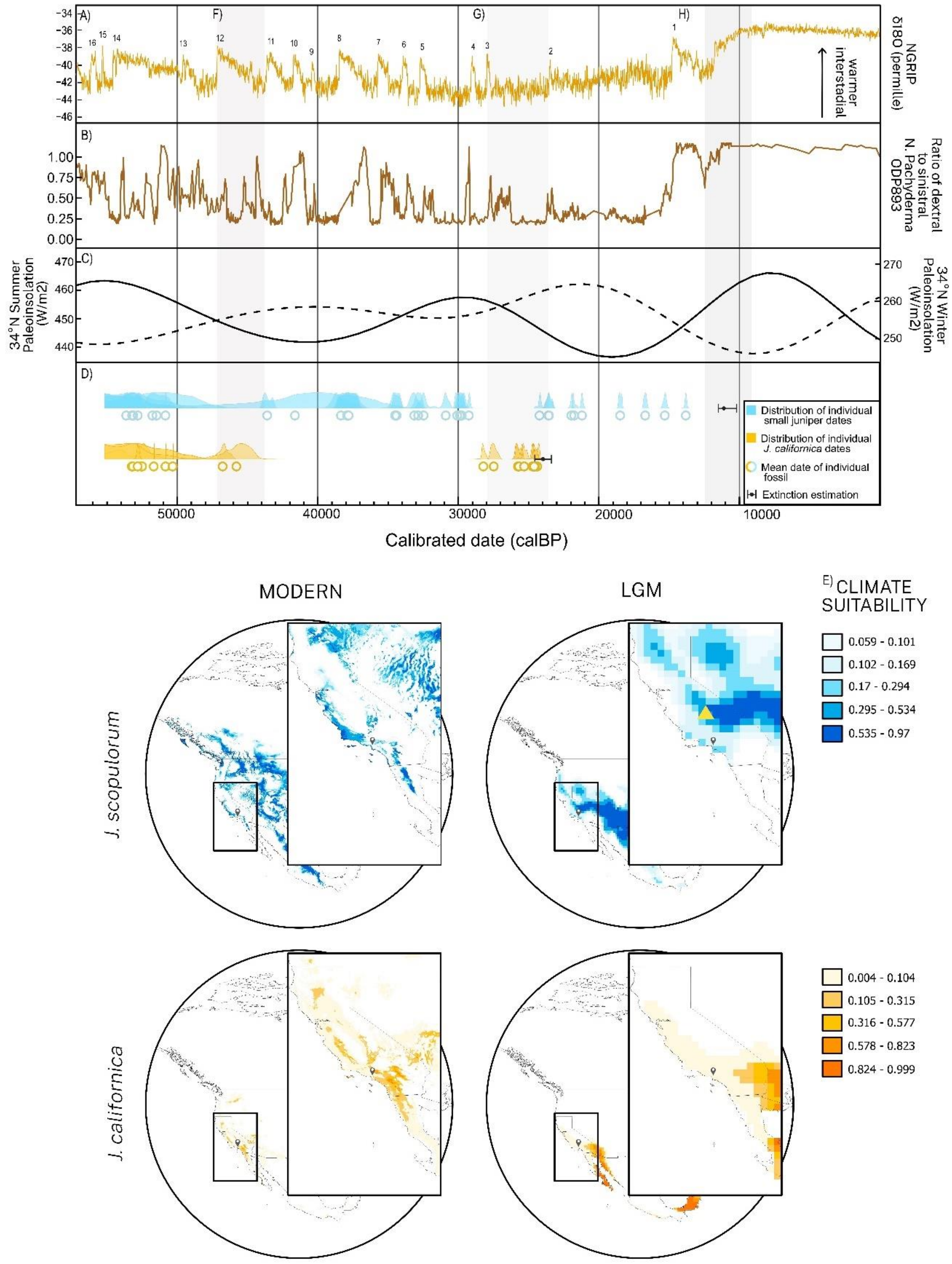

Figure 3-7: A) NGRIP δ^{18}*O record and Greenland interstadial (GI) numbers (Rasmussen et al. 2014) B) Ratio of dextral to sinistral N. pachyderma in Santa Barbara Basin core ODP-893 (Hendy et al. 2007) C summer/winter insolation for 34° N (Laskar et al. 2004) D) Radiocarbon date distribution, means and extinction estimates for J. californica and J. cf. scopulorum E) Modern and LGM SDMs for J. californica and J. cf. scopulorum. Owens Valley fossil J. scopulorum location indicated with a yellow triangle.*

dated to 21,434 cal BP, during the LGM and (Koehler & Anderson, 1994) and 12,156 BP (Wigand, 2002) during the Younger Dryas (figure 3-7) supporting the SDM suggested expanded range of *J. scopulorum* into Eastern California.

The combination of leaf scale and branchlet morphology, 2D and CT image analysis of seeds, and hindcasted SDMs suggest *J. scopulorum* as the most likely modern identification of the LBTP fossil juniper, making it the most extreme example of extirpation in the LBTP flora thus far. An identification of *J. scopulorum* however, cannot be made with complete certainty with the data at hand owing to the complexity introduced by CT image analysis and the geographic particularities of where LBTP is located.

Given the past and present high floral diversity of California (Ackerly, 2009; Axelrod, 1965, 1973, 1978; Axelrod & Raven, 1978; Baldwin, 2019; Bittman, 2003; Burge et al., 2016Millar, 1986), in addition to *J. scopulorum'*s ability to hybridize on the edges of its range with overlapping populations (Adams, 2014), this study can't entirely rule out the possibility that fossil specimens represent a new (and now extinct) species of the *virginiana* group of multi-seeded, entire-leaf junipers. However, given the close alignment of seed and leaf morphological features and abiotic niche space to *J.* scopulorum, for the purpose of this study, we will be referring to the fossil species as *Juniperus* cf. *scopulorum*. Today, a species that can be considered weedy, invading disturbed areas similarly to *J. virginiana* and can generally be found on dry, rocky, mountainous soil (Adams, 2007).

3.6.2 Radiocarbon chronology and implications for climate

Radiocarbon dates of fossil seeds (Appendix table A-2; Figure 3-7) revealed surprising patterns of a long-term presence of both *J. californica* and *J.* c.f. *scopulorum* locally at LBTP until the Holocene. While both juniper species appear to coexist prior to ~48 ka, radiocarbon dates indicate two breaks in preservation of *J.* cf. *scopulorum* seeds, one at ~48 ka followed by exclusive preservation of *J. californica* seeds from ~48-44.5 ka and another at ~29.3-25.2 ka, again replaced by *J. californica.* These patterns of species representation suggest niche differences or competitive interactions between the two juniper species and present implications for local climate effects as both species possess physiological differences related to water-stress.

3.6.3 Juniper species and climate

While juniper as a genus are known to be relatively drought resistant, a study of hydraulic traits of 14 juniper species from the United States and Caribbean, including *J. scopulorum* and *J. californica*, found *J. californica* and other serrate leaved junipers to be 34-39% more resistant to xylem cavitation from water stress than the group of entire leaved junipers that includes *J. scopulorum* (Willson et al., 2008b). In this study, *J. californica* was found to be one of the most resistant to water-stress induced xylem cavitation of all the North American junipers (Mahaffey et al., 2020; Willson et al., 2008a). As smooth margined juniper and serrate margin juniper have demonstrably distinct abilities to cope with water-stress and are more likely to be found in environs suited to those abilities, mesic and tropical locations for smooth margined juniper and drier habitats for serrate margined juniper, their presence and reciprocal alterations through time at LBTP in relation to one another, is likely an indicator of moisture availability.

There is some indication that temperature has also played a role in the timing of juniper presence at LBTP. In the modeled outputs, the top contributor to modeled distribution of *J. scopulorum* was the mean temperature in the warmest quarter, compared to *J. californica* where minimum temperature in the coldest month contributed most to modeled distribution. This is unsurprising, considering *J. scopulorum* is largely considered a cold adapted species (Adams, 2014). Additionally, the record of fossil *J.* cf. *scopulorum* after 50 ka appears to coincide with periods of reduced seasonality in insolation (Figure 3-7).

3.6.4 Post 50 ka Reciprocal Relationship of Juniper Species and Implications for Megadrought

While the two juniper species appear to exist contemporaneously prior to ~50 ka, there is an early shift in the behavior of juniper presences in the record. *J. californica* appears without *J.* cf. *scopulorum* from ~48-44.5 ka. This first instance of *J. californica* dominating the record, coincides with a DO warming event (Greenland interstadial 12) (figure 3-7) registered in the GISP2 δ^{18}O and NGRIP δ^{18}O isotope record from Greenland (Grootes & Stuiver, 1997; Rasmussen et al., 2014). These events are characterized by abrupt periods of warming followed by gradual cooling linked to size of the Northern Hemisphere Ice Sheets, atmospheric CO_2, and the strength Atlantic meridional overturning circulation (AMOC) (Zhang et al., 2014). These millennial-scale warming events are registered strongly in nearby marine core ODP 893 from the Santa Barbara Basin (SBB). From 65-25 ka there are increases in sub-polar planktonic-foraminiferal assemblages indicative of a weakened CC and SST changes of 3-5˚C (Hendy & Kennett, 2000). This same event registers distinctly in the high elevation Baldwin Lake core from southern California as an increase in total organic matter and increase in arboreal pollen (Glover et al., 2017, 2020). The Owens Lake vegetation of Eastern California records a decrease in juniper pollen during this period (Woolfenden, 1996).

Similar patterns are observed at the beginning of the subsequent period of *J. californica* dominance during MIS2 with Greenland interstadial 3 (GIS3). This is event is closely followed by a two-thousand year megadrought identified in the LE record ending at 25.7 ka (Heusser et al., 2015; Kirby et al., 2018). The MIS2 period of *J. californica* dominance aligns with and continues uninterrupted across GIS3 and the LE megadrought. The well-defined nature of *J. californica* phases coupled with the later distinct overlap with the MIS2 megadrought (discussed further in the next section), may suggest the presence of an earlier period of megadrought in MIS3, spanning approximately ~48-44.5 ka. Previous work on LBTP juniper wood has identified insect galleries similar to colonization by extant scolytines and buprestids, including those obligate to *J. scopulorum* that were dated to 42 ka and interpreted as evidence of environmental stress (Holden & Harris, 2013b) may support a period of extreme drought during MIS3.

J. cf. *scopulorum* replaces *J. californica* at 44 ka and remains the sole juniper species preserved at LBTP for the remainder of MIS3. It is interesting to note that this replacement coincides with a reduction of seasonality and lower summertime insolation (figure 3-7C). *J.* cf. *scopulorum*'s alignment with orbital patterns of insolation maxima and minima may support the MaxEnt's estimated top contributor of modeled distribution as mean temperature in the warmest quarter.

The beginning of MIS2 (29-14 ka) is marked by another abrupt replacement of *J.* c.f. *scopulorum* with *J. californica,* from ~29.3-25.2 ka. This period of replacement is partially contemporary an event registered in Lake cores from LE that indicate a period of megadrought from 27.6-25.7 ka demonstrated by a drop in lake level and shifts in surrounding vegetation to more xeric taxa (Heusser et al., 2015; Kirby et al., 2018). This pattern has been interpreted to be present in other Southern Californian cores including a higher elevation site in the nearby San Bernadino Mountains (Baldwin Lake), as well as Lake Manix in the Mojave desert, fed by water from the San Bernadino Mountains (Glover et al., 2017; Kirby et al., 2018; Reheis et al., 2015). This 2000 year period of drought coincides with increased sea surface temperatures (SST) in the Santa Barbara Basin (Hendy, 2010; Heusser et al., 2015).

While the reappearance of *J. californica* in the fossil record at LBTP occurs nearly 2 ka earlier than Elsinore. It's possible that the reorganization of plant communities at LBTP from the more mesic *J.* c.f. *scopulorum* to the extremely drought tolerant *J. californica* is in response to the same extended period of drought, favoring physiology that is more resistant to xylem-cavitation under increased water stress. Today *J. californica* is the only juniper found in the region surrounding LE. It's possible that past declines of juniper in the pollen record were recording a different, more abundant species at the time, like *J. scopulorum.*

At 25 ka *J.* c.f. *scopulorum* reappears in the LBTP record, once again abruptly replacing *J. californica*. The reemergence of *J.* c.f. *scopulorum* again occurs as summer insolation declines. *J. californica,* with a median estimated extinction period of 25 ka, does not reappear in the record again and is no longer present in the Los Angeles Basin. It's closest population today is on the NE end of the Verdugo Mountains 20 km NE at an elevation of 325 meters.

3.6.5 Extirpation of Juniper in the La Brea Tar Pits Region

As noted above, *J. californica* disappears from the LBTP fossil record in MIS2 at 25 ka. The LGM model of suitable habitat for *J. californica* shifts further south than its modern extent, possibly in response to cooler temperatures. Summer temperatures were cool enough in Southern California from 18–20 ka, 15–16 ka, and 12–13 ka for glaciers to form in the San Bernadino mountains (Owen et al., 2003). The final appearance of *J.* cf. *scopulorum* at ~15.2 ka and estimated time of extinction of 13-11.7 ka corresponds with the warming associated with the Ållerød interstadial (GI 1). It is worth noting the large difference in seasonal insolation that occurs during this interval as it follows post 50 ka patterns of *J.* cf. *scopulorum*'s response to orbital patterns. A noticeable increase in SST across the Southern California Margin is also recorded during the Ållerød interstadial, 14.1–12.9 ka (Hendy, 2010). Increased summer insolation, reduced precipitation, and warmer atmospheric temperatures may have not been ideal for the persistence of *J.* cf. *scopulorum* at LBTP. A difference in global annual temperatures between the glacial and interglacial period is estimated to be 3.5 - 5.2˚C similar to projected future temperature shifts in North America (Willis & MacDonald, 2011) placing *J.* cf. *scopulorum* as a possible paleo-casualty of 21st century aligned climate shifts. However, previously, similar changes had resulted in the replacement of *J.* cf. *scopulorum* with *J. californica*, why at this point in the record, do we see the disappearance of juniper entirely?

One highly notable occurrence coinciding with the disappearance of both juniper species in the fossil record is the Late Pleistocene extinction of megafauna. The last forty thousand years of the Pleistocene saw the disappearance of the majority of the globe's megafauna (animals weighing >40 kg). North America alone saw the extinction of approximately 34 genera of megafauna in addition to the loss of many smaller animal species. Most of these disappearances occurred in the period between last glacial maximum (LGM) and the Holocene interglacial (Jeffers et al., 2018; Koch & Barnosky, 2006; Meltzer, 2020), with the last megafaunal species disappearing by approximately 10 ka (Barnosky & Lindsey, 2010; Gill et al., 2009; Koch & Barnosky, 2006; O'Keefe et al., 2009).

Such a drastic change to the ecological setting would have certainly had a dramatic impact on flora. Disappearance of megafauna would have greatly impacted nutrient cycling, limiting key nutrients like phosphorous and nitrogen in the soil (Doughty et al., 2013; Faith, 2011; McLauchlan et al., 2013). Lake records in Indiana and Ohio suggest the disappearance of browsers increased woody shrub and tree growth, increasing fuel loads and fire frequency (Gill et al., 2009, 2012). The presence of large herbivorous fauna likely encouraged more open landscapes, their disappearance precipitating more closed canopy forests at the start of the Holocene (Gill, 2014).

Juniper is generally considered unpalatable by most modern, large, herbivores (Launchbaugh et al., 1997) and when consumed by modern cattle has been found to increase the likelihood of aborted pregnancy (Gardner et al., 2010). There are modern herbivores that occasionally browse juniper such as deer, sheep, and goats (Adams et al., 2013); Ice Age megaherbivores may have done the same. Isotopic evidence from La Brea herbivore species suggests a mixed grazing and browsing diet that may have included juniper (Coltrain et al., 2004; Jones & Desantis, 2017). In modern times, juniper populations have been observed to expand with the presence of grazing throughout the year in addition to suppressed fire regimes (Van Auken, 2008).

A recent paper establishing a higher resolution chronology of faunal material at LBTP estimated the extinction point for the top five megaherbivores at LBTP to be 13.02 ka, aligning their disappearance with the extirpation of *J.* cf. *scopulorum* (O'Keefe et al., *submitted for publication*). The same study argues an increase in fire around 13 ka in Southern California registered at LE and off the coast on Santa Rosa Island (Kennett et al., 2008) presents a problem of adequate sources of ignition if humans are not being considered (O'Keefe et al., *submitted for publication*).

Fire rotation intervals for junipers in the southwest have been calculated ranging from ~400-300 years (Floyd et al., 2004; Huffman et al., 2008). Suppression of fire in the Southwest has been linked to expansion of piñon-juniper woodlands, with less fire translating to increased opportunity for juniper to colonize (Miller & Tausch, 2001; Miller & Wigand, 1994a; Romme et al., 1998). *J. scopulorum* is especially susceptible to death from fire, due to its fibrous, thin, bark and volatile oils in branches that frequently reach the ground (Burns & Honkala, 1990). Studies on modern die back of juniper woodland identify rising temperatures, prolonged drought, insects, and increased fire frequency and intensity on woodland survival (Flake & Weisberg, 2019; Floyd et al., 2004, 2015). 700-500 years ago the combination of drought and increased fire activity resulted in a dramatic decrease in juniper woodland in the Great Basin (Miller & Wigand, 1994b). It's possible that the combination of rising temperatures, increasing aridity, more frequent fires (natural or human ignited), and the disappearance of large-bodied grazing herbivores at the end of the last glacial led to the disappearance of both *J. californica* from the Los Angeles Basin and *J.* cf. *scopulorum* from California.

3.7 Conclusion

Historically, native junipers have not be found in the region of LBTP. Detailed taxonomic analysis of juniper seeds suggests that two species, *J. californica* and *J.* cf. *scopulorum* were present at the LBTP during the late Pleistocene from ~55 ka to ~12.3 ka. *J. californica* appears to only be dominant during warmer and drier periods and *J.* cf. *scopulorum* in periods with reduced summer insolation post 50 ka. These variations in juniper species dominance suggest two prolonged warm droughts at ~48-44.5 ka and ~29.3-25.2 ka. *J. californica* is replaced by *J.* cf. *scopulorum* for the last time at 25 ka, this absence is likely made permanent in response to the same environmental shifts that precipitate the extirpation of *J.* cf. *scopulorum* at 12.3 ka. Increased temperatures, reduced precipitation, a disappearance of large-bodied grazing herbivores and a regional spike in fire frequency, especially, would have pushed both juniper species out of the Los Angeles Basin. The fossil record of juniper at LBTP highlights the complex and highly individualistic response of plant species to climatic and environmental change, patterns that can be observed especially well through the identification and radiocarbon dating of preserved macro-fossils.

3.8 References

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Chapter 4 55,000 Year History of California Plant Community and Ecological Response to Climate

4.1 Abstract

The La Brea Tar Pits (LBTP) is one of the most paleontologically prolific fossil deposits on the planet for biota from the Late Pleistocene and Holocene. Despite this, plant fossils from the asphalt deposits have been notably understudied throughout the history of excavation. This study uses accelerator mass spectrometry (AMS) radiocarbon dating of plant macrofossils to reconstruct a timeline of plant presence in the Los Angeles Basin for the past ~55 ka. This timeline provides a rare local-scale record of coastal Southern California vegetation with high taxonomic resolution to address important gaps in our understanding of regional environmental changes. Addressing whether plant species presences changed throughout the Late Pleistocene and Holocene in the Los Angeles Basin and if those changes correspond to known shifts in climate or megafaunal presence. The 55 ka record of LBTP vegetation reveals at least 8 phases of vegetation change. More broadly LBTP vegetation transitions from closed cone pine forests during marine isotope stage 3 (MIS3) to more open oak-juniper woodland in late MIS3 /MIS2 to a new assemblage of woody broadleaf tree and herbaceous taxa appearing at the end of MIS2 and continuing into the modern period. These shifts are responses to interactions between drought, increasing aridity, decreasing atmospheric CO_2 concentrations, and megaherbivore presence. Orbital variation drives a lot of change to LBTP species composition as does variability in atmospheric temperature and coastal sea surface temperatures (SST). The terrestrial record of vegetation at LBTP provides a much-needed long-term record of environmental change

for the Los Angeles Basin during the Late Pleistocene and Holocene and demonstrates remarkable sensitivity in species response to shifting climatic and ecological conditions.

4.2 Introduction

The La Brea Tar Pits (LBTP) in Los Angeles, California has played a pivotal role in defining North American mammalian biota of the Late Pleistocene (Bell et al., 2004). Asphalt impregnated fossil bones of Ice Age megafauna have helped shed light on the life histories, ecology, and disappearance of charismatic megafauna like sabertoothed cats (*Smilodon fatalis*), dire wolves (*Aenocyon dirus*), and Columbian mammoths (*Mammuthus columbi*) (Adli et al., 2015; Akersten et al., 1988; Balisi & Van Valkenburgh, 2020; Binder et al., 2002; Brown, Balisi, et al., 2017; Chester Stock, 1992; Coltrain et al., 2004; DeSantis et al., 2019; Feranec et al., 2009; F. R. O'Keefe et al., 2022). In LBTP's history of research there is a notable scarcity of studies on LBTP flora (Frost, 1927; Gerhart et al., 2012; Templeton, 1964; Ward et al., 2005; Warter, 1976) despite lignose and cellulose preserving readily in asphalt. The lack of data on LBTP plants has left significant gaps in our knowledge of the environmental transitions that took place in the Los Angeles Basin during the Late Pleistocene and Holocene.

As primary producers, plants serve as an inseparable anchor to the larger food web of LBTP. No shift in fauna can be fully understood without addressing changes to the surrounding plant life first (MacDonald et al., 2012). The spatially fixed nature of plants also makes them powerful proxies for climate. Their presence at a site suggests the environmental conditions for which they are specially adapted are being met (Ackerly, 2009), allowing for reconstructions of environmental conditions through time if presence of species or genera at a given period are known (Blois et al., 2013; Veloz et al., 2012). Without a timeline of plant presence for LBTP, crucial information on climate and ecological setting is missing.

The abundance of plant macrofossils, or plant material visible with the naked eye, at LBTP uniquely situates it to address these gaps in environmental knowledge with both high taxonomic resolution and a relatively continuous record across a period spanning from ~55 ka to present. Unlike palynomorph based records, plant macrofossils such as cones, seeds, leaves, and wood have the potential of identification down to species level (Jackson et al. 1997; Jackson & Weng 1999; Follieri 2010) but are generally far less likely to be preserved in contexts that allow for detailed reconstructions across time. The asphalt-rich sediments of the LBTP's are an exception in terms of providing a high potential for plant fossil preservation.

The source of LBTP's asphalt seeps is Miocene age, oil bearing, sedimentary rock, approximately 450 meters below the modern surface. Surficial hydrocarbon pooling resulting from oil travelling upward through cracks and fissures has trapped and preserved bone, calcium-carbonate shell, insect chitin, and cellulose for the past ~55 ka (Chester Stock, 1992). In LBTP's past, seasonal fluvial deposition of sediments over seeps, later saturated by renewed seep flow, ensured protection and burial of previously trapped biotic material and continued opportunity for biotic entrapment.

The unique taphonomic conditions created by the asphalt seeps at LBTP allow for abundant preservation of plant macrofossils across the last ~55 ka. It's location within a relatively constrained drainage basin (figure 4-1) paired with the highly localized entrapment patterns of plant macro-material in asphalt seeps provides a spatially specific, local-scale record of vegetation. Lack of preserved stratigraphy within the seeps necessitates dating of individual specimens (Friscia et al. 2008; Holden et al. 2017).

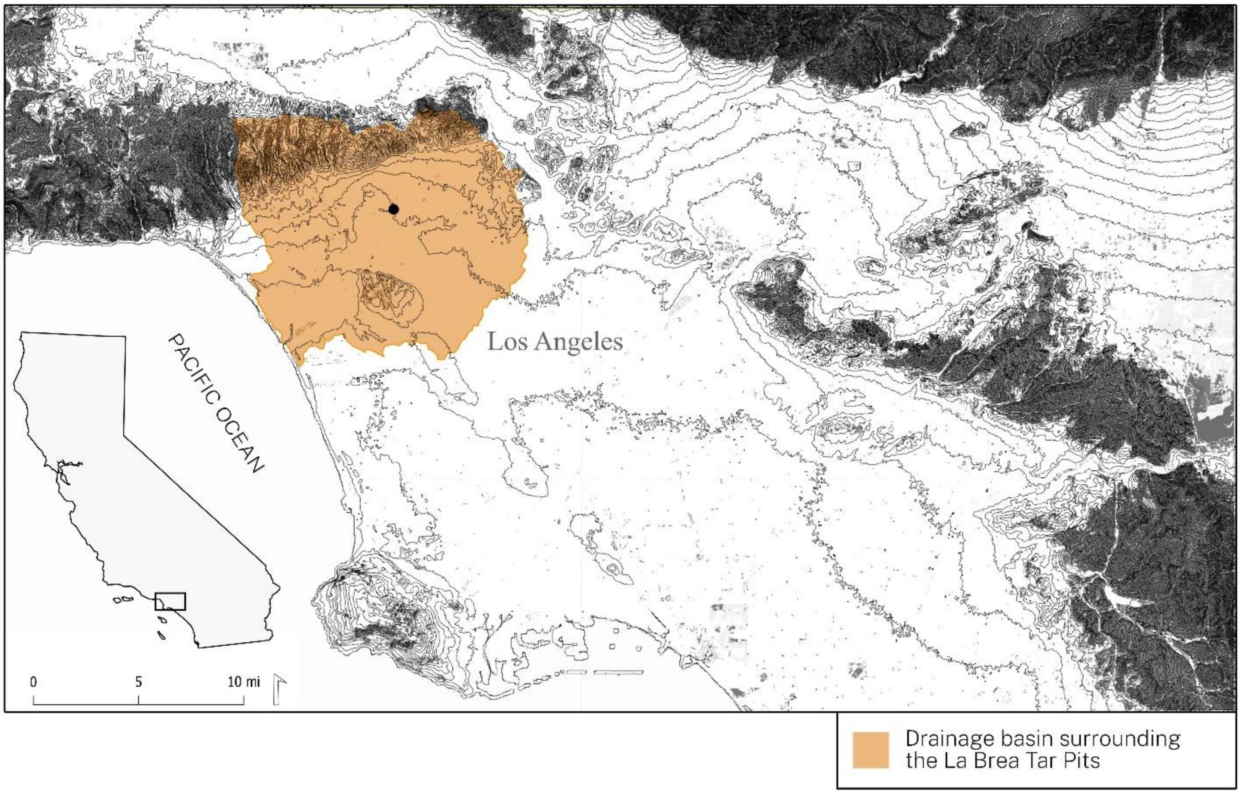


Figure 4-1: Topographic map of the Los Angeles basin with La Brea Tar Pits (LBTP) marked with a black dot. The drainage basin surrounding the LBTP is highlighted in orange and marks the extents plant material can be transported by water from.

This study presents a chronology of plant species presence at LBTP through identification and AMS radiocarbon dating of 188 asphalt preserved plant macrofossils. By establishing a timeline of LBTP flora we can address whether there were differences in plant species presence across the ~55 ka of preservation at LBTP, if observed shifts in plant species presence occurred in response to known climatic events, and if the timing of megafaunal disappearance at LBTP coincided with shifts in plant presence. This record, added to recent, growing efforts to address the smaller, important, environmental indicator fossils of LBTP (Fox et al., 2019; Glover et al., 2018; Holden et al., 2017; Mychajliw, Rice, et al., 2020), provides important baseline data to address critical gaps in our understanding of the environmental events of the Late Pleistocene and Holocene.

4.3 Study Site

LBTP is located in coastal Southern California (34.063598, -118.356275) within the Los Angeles Basin on the traditional, ancestral and unceded territory of the Gabrielino/Tongva peoples. A Mediterranean climate regime, the site experiences warm, dry summers, and cool, wet winters. LBTP receives annual rainfall amounts of 353 mm (208 mm during the coldest quarter) and a mean annual temperature of 11.3°C according to the WorldClim climate database (averaged from the years 1970-2000) (Fick & Hijmans 2017).

Sea surface temperatures (SST) off the coast of California effect the climate over the land and (MacDonald et al., 2016) are influenced by strength of coastal currents. The California Current (CC) brings cool and nutritionally poor water south towards the equator and is impacted by northerly winds associated with seasonal migration in the North Pacific High (NPH) pressure cell. The Davidson current runs counter to the CC poleward, carrying warmer water to the north. In Southern California, the Channel Islands and Southern California Bight disrupt flow of equatorward and poleward currents, with the CC moving west away from the coast and the Davidson undercurrent flowing into the Southern California Eddy (Hendy, 2010)

The asphalt seeps and deposits are located in the northern section of the geologically young Los Angeles Basin. The sedimentary basin is broadly defined by the Santa Monica Mountains to the north, the Elysian, Repetto, and Puente Hills to the east, and Santa Ana Mountains and San Joaquin Hills to the south (Lamar, 1970; Yerkes, 1965). Underlying Pliocene and Miocene age sedimentary rock, formed under marine conditions when the basin was submerged, act as reservoir rock to the basin’s numerous oil deposits (Blake, 1991). Seeping occurs from submerged oil deposits across the basin with gas migration along faults, though LBTP remains the most visually prominent example of seepage (Etiope et al., 2017).

LBTP exists in a smaller drainage basin encompassing the eastern Santa Monica Mountains, Elysian Hill, and Baldwin Hills (figure 4-1). Remnant native vegetation surrounding the site is composed of fragmented sites of mixed chaparral and coastal sage scrub on developed hillsides (Swenson & Franklin, 2000). Its proximity to the 6th street fault and resulting tectonic activity, provides opportunity for hydrocarbons to migrate upward and pool at the surface, forming sticky “fly paper” like traps in warmer weather. These traps have formed for the past ~55 ka.

4.4 Methods

4.4.1 Fossil Identification

The LBTP collections house previously identified, accessioned plant macrofossils, unidentified material collected directly from excavations, and cleaned, unsorted, bulk matrix from specific excavation grids. This project worked with material from all three collection contexts. Both unknown or previously identified specimens were identified or verified using modern reference collections and photographed individually for collection records before dating. LBTP’s in house modern reference collection was used for identification and supplemented by comparisons to specimens at the UCLA herbarium and Rancho Santa Ana Botanic Garden’s herbarium and seed conservatory. Identifications were made using a stereo microscope or compound fluorescent microscope (figure 4-2). Digital image analysis with open-source digital image analysis software “ImageJ” (Schneider et al., 2012) was used in conjunction with principal component analysis (PCA) to better understand relationships between morphological measurements and species divisions for fossils that were not readily identifiable by clearly distinguishable diagnostic features.

4.4.2 Radiocarbon

200 plant fossil specimens were AMS radiocarbon dated, 12 were destroyed in processing, and 188 yielding successful dates. To avoid asphalt contamination and a resulting bias in radiocarbon dates, special attention was paid to thoroughly removing asphalt from the sampled fossil material. Specimens were prepped at the UC Irvine W.M. Keck Carbon Cycle Accelerator Mass Spectrometer Facility. Samples were treated with repeated sonications in a 2:1 toluene: methanol solution (Fuller et al., 2015), followed with an acid-base-acid wash with 1N HCL and 1 N NaOH. Acid-base-acid protocol was followed by a bleach treatment with chlorine dioxide using a 1:1 mixture of 1 N HCl and 1 M $NaClO_2$ (Mychajliw, Rice, et al., 2020). Samples were bleached to holocellulose to visually ensure the removal of all asphalt. Radiocarbon calibrations and plots were made in OxCal 4.3 using the IntCal20 calibration curve (Bronk Ramsey, 2009; Reimer et al., 2020).

Figure 4-2: Fossil seeds and leaves of J. cf. *scopulorum (left). Seed imagery taken under a stereo microscope and analyzed using ImageJ. Juniper leaves (right) imaged using a compound fluorescent microscope and identified by cell shape and leaf margin.*

4.4.3 Statistical Analysis

To address change in composition through time we use the Jaccard similarity coefficient to calculate the ratio of shared species to total species. Given the possibility that taphonomic processes in the seeps can bias the representation of plant material, we chose to avoid similarity or dissimilarity measures including abundance and the binary Jaccard similarity coefficient offers more flexibility in handling possible missing species (Cao, 2018).

Coexistence analysis was carried out with the ‘climate reconstruction analysis using likelihood estimation’ (CRACLE) method (Harbert & Nixon, 2015, 2018) to isolate dominant climate factors influencing community makeup. A form of estimation of climate from vegetation or ECV approach, CRACLE uses explicit species occurrence data for coexistent species and selects the most likely climate parameters for a given site, based on maximizing the univariate empirical joint likelihood of species’ climatic coexistence.

In this project’s case, coexistence analysis allows for quantitative method of defining likely environmental conditions for a given grouping of species. This provides a comparative tool illustrating how species environmental demands might change through time. Because outside factors other than climate, such as atmospheric CO2 and edaphic conditions may also impact plant composition, climate estimates cannot be treated as independent climate data.

To construct sampling points for analysis, probability distributions of 95.4% were binned into 2000-year time bins (Carleton & Groucutt, 2021). Overlapping probability distributions within 95.4% within a single bin are treated as a species presence and included in the maximum likelihood estimation (MLE) for that 2000-year period. Means of MLE were calculated for mean annual temperature (MAT), annual precipitation, and precipitation of the coldest quarter using species observation data from iNaturalist and the Global Biodiversity Information Facility (GBIF) alongside WorldClim climate data (Fick & Hijmans, 2017b). Observations were restricted to non-cultivated and research grade points.

4.5 Results

Within the 188 radiocarbon dates, 54 results were too close to background and yielded only the lower limit of the possible date. Of those, 51 dates are in phase F1, 3 are in F2 and F3.

At least 26 taxa were identified (Appendix table A-3). Probability distributions of radiocarbon dates are presented in figure 3 ranging from ~55 ka to present figure 3). Bishop pine (*Pinus muricata*), Monterey pine (*Pinus radiata*) and grey pine (*Pinus sabiniana*) are grouped together within figure 3 for ease of interpretation. Coast live oak (*Quercus agrifolia*), and California scrub oak (*Quercus* cf. *dumosa*) are grouped under *Quercus* to accommodate some uncertainty in individual identifications. The frequency of dates is highest during marine isotope stage (MIS) 3 (57-29 ka), while an absence of plant material is noted from 10-3 ka.

The majority of identified specimens have current natural ranges within the coastal region of Southern California today with three exceptions: Rocky Mountain juniper (*Juniperus scopulorum*), Monterey cypress (*Hesperocyparis macrocarpa*), *Pinus radiata,* and *Pinus muricata*. Pine specimens did not date younger than 48 ka suggesting a shift in moisture regime at this time. Cypress specimens similarly do not date younger than 43 ka. Species richness is at its highest during MIS 3 diminishing to 1-2 species of *J. scopulorum, Quercus* (primarily *Q. agrifolia*), or *J. californica* for much of MIS 2 (29-14 ka), suggesting a more open landscape at this time. A cluster of dates of boxelder maple (*Acer negundo*) occurs from 16.25-15 ka at the close of MIS 2. It's followed closely by the re-appearance of elderberry (*Sambucus mexicana*). The start of the warm interstadial, the Bølling-Allerød, sees the disappearance of both *J. scopulorum* and *Acer negundo*. *Quercus agrifolia,* California sycamore *(Platanus racemosa),* and common madia *(Madia elegans)* are present during the warming period of the Bølling-Allerød at the start MIS 1, from ~14-13 ka. They are followed by clustered tarweed (*Deinandra fasciculata*) and grasses during the Younger Dryas. A substantial gap of preserved plant material

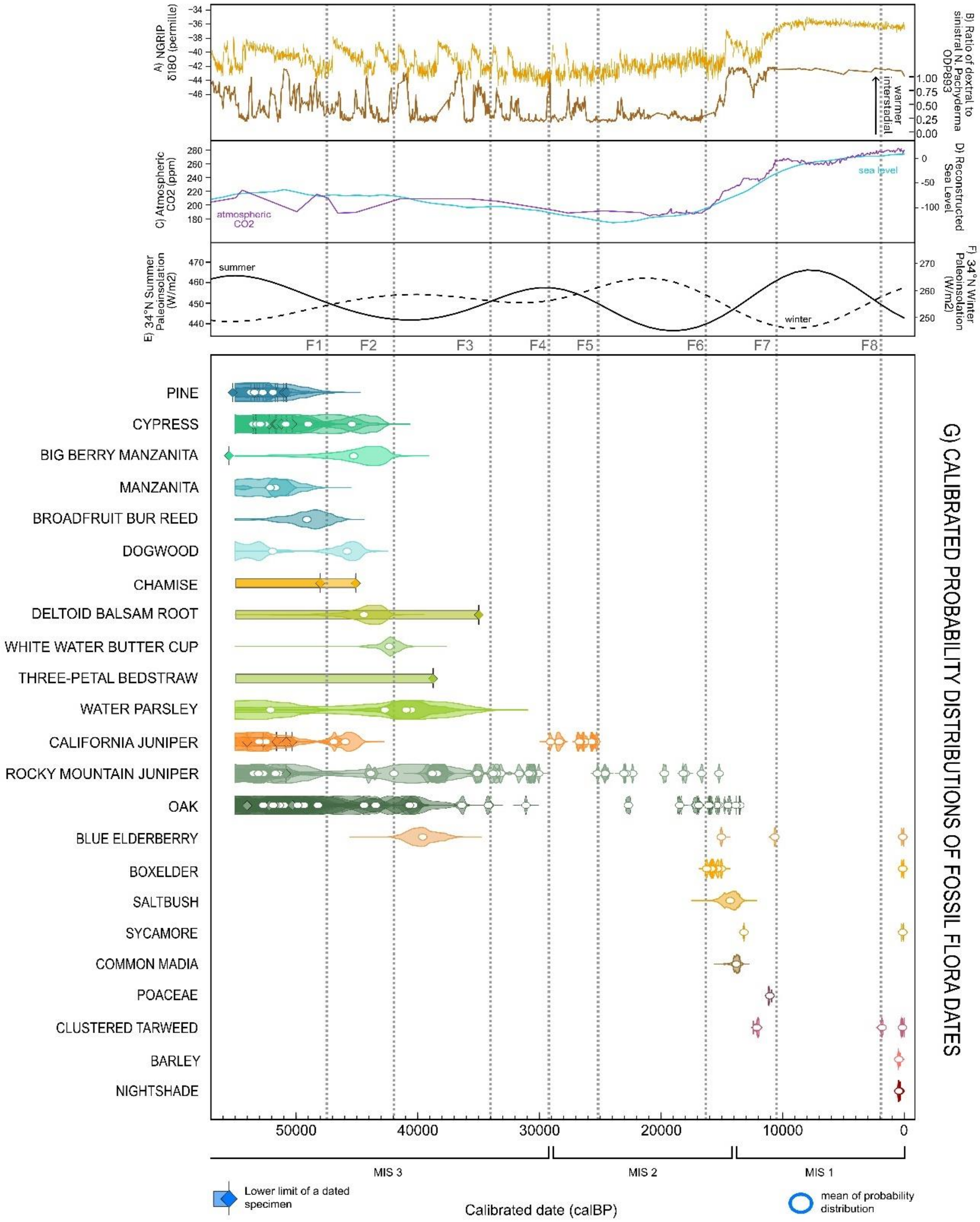


Figure 4-3: Fossil plant radiocarbon probability distributions plotted against A) NGRIP $\delta^{18}O$ record and Greenland interstadial (GI) numbers (Rasmussen et al. 2014) B) Ratio of dextral to sinistral N. pachyderma in Santa Barbara Basin core ODP-893 (Hendy et al. 2007) C) Atmospheric CO2 ppm (Luthi et al. 2008) D) Sea level reconstruction (Spratt and Lisiecki 2016) E-F) summer/winter insolation for 34° N (Laskar et al. 2004) G) Calibrated probability distributions of fossil flora dates. Means of distributions are indicated by circles, diamonds represent specimens where only a lower limit of the date was ascertained F1-F8) Floral phases, dotted lines indicated points of change.

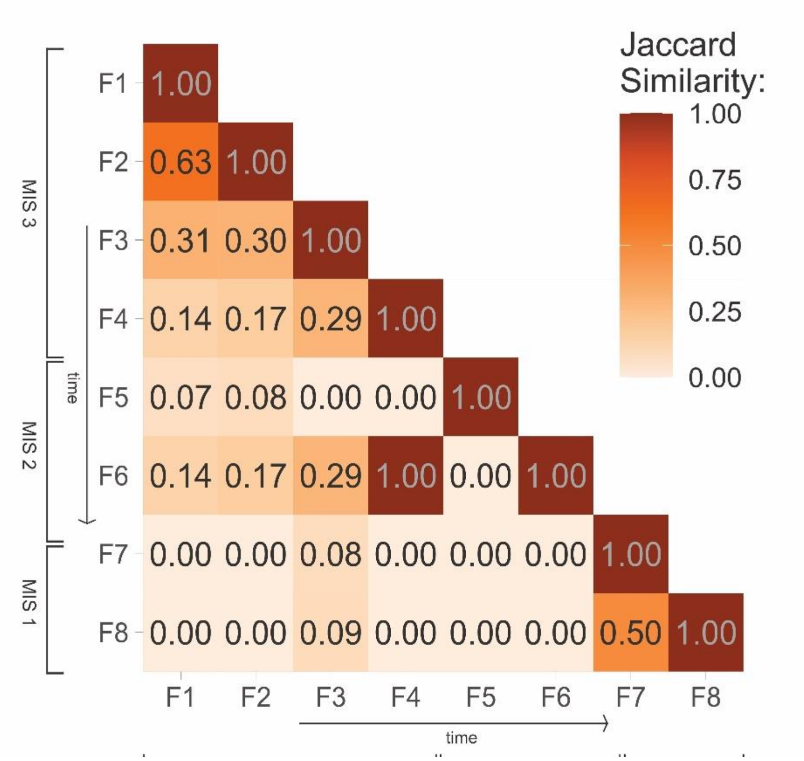
exists between a specimen of S. nigra dated to 10.7 ka and a D. fasciculata dated to 1.9 ka. Several substantial reorganizations of plant communities occur across the 55,000-year time frame. Shifts in plant community makeup appear to occur at 47.4 ka, 42 ka, 34 ka, 29.2 ka, 25.1 ka, 16.25 ka, and 10.7 ka (Table 4-1). These shifts are used to divide the chronology into 8 floral phases. Floral phase 7 (F7) and F8 are interrupted by the absence of plant fossils from 10.7-2 ka.

Table 4-1: Floral Phases Identified in LBTP Record

DATE (KA)	**FLORAL PHASE**	**DESCRIPTION**	**KEY TAXA**
~55-47.4	F1	Closed cone pine forest and chaparral	Closed cone pine forest species: *Pinus radiata, Pinus muricata.* Other conifers: *Pinus sabiniana, Hesperocyparis macrocarpa, Juniperus californica, Juniperus* cf. *scopulorum.* Chaparral species: *Arctostaphylos* ssp., *Adenostonum fasciculatum, Quercus agrifolia*, *Quercus* cf. *dumosa*
47.4-42	F2	Cypress-oak-juniper chaparral, wetland/ riparian	Conifers: *Hesperocyparis macrocarpa, Juniperus californica, Juniperus* cf. *scopulorum.* Chaparral species: *Arctostaphylos glauca*, *Adenostoma fasciculatum, Quercus agrifolia, Quercus* cf. *dumosa.* Wetland/ riparian species: *Cornus sericea, Sparganium eurycarpum, Ranunculus aquatilis, Oenanthe sarmentosa*
42-34	F3	Mesic oak-juniper woodland	Juniperus scopulorum, *Quercus* ssp., *Balsamorhiza deltoidea, Ranunculus aquatilis, Galium trifidum, Oenanthe sarmentosa, Sambucus nigra*
34-29.2	F4	Oak-juniper woodland	*Juniperus scopulorum, Quercus* ssp.
29.2-25.1	F5	California juniper	Juniperus californica
25.1-16.25	F6	Oak-juniper woodland	*Juniperus scopulorum, Quercus* ssp.
16.25-10.7	F7	Late-Glacial/Holocene transition, woody/herbaceous	Woody species: *Acer macrophyllum, Sambucus nigra, Platanus racemosa, Atriplex sp.* Herbaceous species: *Madia elegans*, Poaceae, *Deinandra fasciculata*
2-MODERN	F8	2 ka-modern	*Acer negundo, Sambucus mexicana, Platanus racemosa*

Pairwise Jaccard similarity values were calculated across floral phases (figure 4-4). Of 28 comparisons 13 scored 0 with no overlap in species. F7 and F8, representing the end of MIS 2 and MIS 1, showed the least similarity to other phases and most similarity to each other (.50). The rest of the phase comparisons score. 31 or less with two exceptions. F4 and F6 have a score of 1, as they share the same species and would likely be a single phase if they weren't interrupted by F5, a period characterized entirely by *Juniperus californica* fossils for 4.1 thousand years. F1 compared to F2 has a similarity score of .63, however, the disappearance of all pine in the transition from F1 to F2 suggests changes to key species and warrants separation. Overall, pairwise Jaccard similarity results support substantial change in composition across time.

Coexistence analysis results (figure 4-5) for MAT indicates fluctuations in temperatures throughout the Late Pleistocene and early Holocene. Averaged, there is a general decline in temperatures from MIS 3 to MIS 2 with temperatures increasing again at the end of the glacial period. MAT for 54-40 ka averages to 13.8°C, this is interrupted by a downward shift to 9.6°C at 38 ka followed by an average of 14.3°C from 36-26 ka. The species present during 24-18 ka indicate an average of 9.9°C. From 16-14 ka the MAT averages to 13.3°C followed by a substantial raise in temperature to 15.6°C at 12 ka. The MAT of 10 ka, 9.0°C, is based off the MAT for the range of a single species (*Sambucus mexicana*) and coincides with the onset of the Younger Dryas. Lack of fossils from 10.7-2 ka prevents reconstruction. Average MAT from 2 ka to present is 15.7°C.



	F1	F2	F3	F4	F5	F6	F7	F8
F1	1.00							
F2	0.63	1.00						
F3	0.31	0.30	1.00					
F4	0.14	0.17	0.29	1.00				
F5	0.07	0.08	0.00	0.00	1.00			
F6	0.14	0.17	0.29	1.00	0.00	1.00		
F7	0.00	0.00	0.08	0.00	0.00	0.00	1.00	
F8	0.00	0.00	0.09	0.00	0.00	0.00	0.50	1.00

Figure 4-4: Chart of Jaccard Similarity Values Compared Across all Floral Phases.

Annual precipitation also sees a decline from MIS 3 into MIS 2 before demonstrating large fluctuations in the post glacial and Early Holocene. From 54-38 ka annual precipitation averages to 612 mm with an anomalous peak of 1101 mm at 48 ka. From 36-34 ka plant communities indicate a reduction in annual precipitation to 414 mm. There is a gradual decline in estimated precipitation 26 ka which similar to MAT fluctuates until 18 ka but has an averaged value of 402 mm. Precipitation rises again from 14-16 ka to a value of 591 mm. It reaches a peak Holocene value of 746 mm at 10 ka. Precipitation averages to 466 mm from 2 ka to present with the 2 ka estimated values of 354 mm reaching closest to Los Angeles's current annual rainfall.

Precipitation in the coldest quarter sees large fluctuations from 54-34 ka with estimated values ranging from 280-530 mm. From 32-16 values remain relatively stable with an average of 171 mm with two lower deviations to the 80s at 24 and 20 ka. Winter precipitation increases with plant compositions from 16-12 ka, reducing again for 10 and 2 ka before increasing to 248 mm at present.

4.6 Discussions

4.6.1 F1: Closed Cone Pine Forest and Chaparral

Phase F1 has the highest number of species represented as well as the highest concentration of radiocarbon dates (not including specimens with only lower limits). This may reflect entrapment bias towards trees and shrubs that produce highly lignified woody fruits, seeds and possess sclerophyllous leaves. F1 is dominated by woody coniferous and chaparral taxa and relatively few herbaceous taxa.

The presence of pine species, particularly *P. muricata* and *P. radiata,* at the beginning of the LBTP record is not unexpected. Closed cone pine forests are thought to have once existed across coastal areas in Southern and Baja California (Axelrod, 1965, 1978, 1980, 1990; Axelrod & Govean, 1996; Axelrod & Raven, 1978; Millar, 1986, 1998). Fossil evidence of closed cone pines from 40-60 ka are present in asphalt preserved Carpinteria flora to the north (Axelrod, 1978; Shaw, 2015). There is also macrofossil evidence from Costa Mesa and Laguna Niguel to the south (Axelrod, 1990; Axelrod & Govean, 1996). Fossils of closed cone pines have been recovered 5.5 km from LBTP within the city of Los Angeles (Axelrod, 1980). Pollen of pine, juniper, cypress is recorded in cores off the coast of Southern California in the Santa Barbara Channel during MIS 3 (Heusser, 1998). These fossil floras are considered an indication of higher moisture availability than at present.

This phase sees high variability in local Sea Surface Temperatures, Northern Hemisphere atmospheric temperatures, and atmospheric CO_2 concentrations (figure 4-3A-D). A maximum of summer insolation is coupled with minimum of winter insolation at LBTP's latitude of 34° N (Figure 3 E,F). Summer insolation maxima are connected to the expansion of the summer monsoon (Barron et al., 2012; Kirby et al., 2006; Kutzbach, 1981) carrying moisture from the Eastern Tropical Pacific and the Gulf of California to the northwest (D. K. Adams & Comrie, 1997). A minimum in winter insolation is connected to increased precipitation from shifting polar jets and can see an increase the frequency of winter storms (Bird & Kirby, 2006; Kirby et al., 2006; Spaulding & Graumlich, 1986). A combination of summer insolation maximum and winter minimum align with heightened lake levels at Baldwin lake, sedimentation, productivity, and arboreal pollen accumulation from 65-52 ka (Glover et al., 2020; Kirby et al., 2006).

4.6.2 F2: Cypress-Oak-Juniper Chaparral, Wetland/ Riparian

The transition to phase F2 is marked by the surprising disappearance of *P. muricata, P. radiata,* and *P. sabiniana*. Cypress, juniper species, oak, manzanita, chamise, and more mesic taxa representative of wetland and riparian environments such as white water buttercup (*Ranunculus aquatilis*) persist in the record. The disappearance of all pine species at LBTP by ~47.4 ka suggests a change in local hydroclimatology as pine is a drought sensitive genus (Martínez-Vilalta et al., 2004). The disappearance of *P. muricata*, in particular, a species still found north of the Southern California Bight and further south in Baja California, may suggest a change in coastal fog or low-lying clouds. It's range today is likely controlled by summer coastal fog patterns (Baguskas et al., 2014; Fischer & Still, 2007; Williams et al., 2008).

Pine's absence in the record is, notably, immediately followed by a temporary absence of dated *J.* cf. *scopulorum* and a period of *J. californica* as the only juniper species present in the record (47.4-45 ka). Chapter 3 argues that periods of dated *J.* cf. *scopulorum* replacement by *J. californica* may be indicative of an extended period of drought for LBTP. While atmospheric temperatures, coastal SSTs and atmospheric CO_2 continue to be extremely variable, this period of juniper replacement coincides with an increase in atmospheric temperatures recorded in the Greenland ice sheet (figure 4-3A). However, Baldwin lake records indicate low lake levels from 52-40 ka (Glover et al., 2017a; Kirby et al., 2006), and a study on LBTP insect galleries found trees weakened by environmental stresses and susceptible to beetle invasion dated to 42 ka (Holden & Harris, 2013a), suggesting more long-term patterns of change. Riparian and wetland taxa from post 45 ka suggest that there is still water present on the site at this time.

4.6.3 F3: Mesic Oak-Juniper Woodland

The transition to F3 is marked by the disappearance of cypress from the record and the first appearance of blue elderberry (*Sambucus mexicana*). The presence of more mesic, wetland/riparian species like *R. aquatilis,* three-petal bedstraw (*Galium trifidum*) and water parsley (*Oenanthe sarmentosa*) still suggest the presence of water on site.

H. macrocarpa has an extremely limited native range to the Monterey Peninsula in the northern end of California's Central Coast, and until recently was thought to have never had made it south of the Transverse Mountain Ranges of Southern California before being reintroduced by humans as a popular landscaping tree (Bartel & Adams, 2018; Terry et al., 2016). The disappearance of cypress at ~43 ka suggests continued aridity, effects that may have combined with stress of decreasing atmospheric CO_2 (Luthi et al. 2008). As atmospheric CO_2 decreased as continental glaciers advanced, the ratio of O_2 to CO_2 increased, decreasing the efficiency of photosynthesis and increasing rates of photorespiration (Sage & Coleman, 2001). In an effort to take in enough CO_2 for photosynthesis, plants would have been forced to hold leaf guard cells, stomata, open for longer losing moisture in the process. In an environment where moisture is not abundant, the stress of low atmospheric CO_2 was likely exacerbated. Stable isotope studies on glacial juniper from LBTP observed signs of carbon starvation and diminished primary productivity (Gerhart et al., 2012; Ward et al., 2005).

While atmospheric CO_2 Is relatively stable through this phase, F3 continues to see great variability in Northern Hemisphere atmospheric temperatures and coastal SSTs. It also sees the dominance of the more mesic *J.* cf. *scopulorum* (Willson et al., 2008a) in the record. Phases featuring *J.* cf. *scopulorum* as the dominant juniper appear to couple with orbital phases with decreased summer insolation and increased winter insolation (figure 4-3E,F) suggesting an affinity with reduced seasonality.

4.6.4 F4: Oak-Juniper Woodland

Quercus and *J.* cf. *scopulorum* are the only two species preserved in the record for F4. This suggests the presence of a juniper-oak woodland vegetation cover. Today, Juniper-oak woodlands are known from Texas and there is one association known from California on

Caliente Mountain overlooking the Carrizo Plain, composed of *J. californica* and Tucker's oak (*Quercus john-tuckeri)*. No extant juniper-oak woodlands are composed of the species present in the LBTP record, making it a novel association. Reduction of species present to these two, may also indicate an opening of landscape. It's likely that grasses or other herbaceous taxa were present at this time, however, low stature and fruit, seeds, or leaves with less cellulose and lignin may be less likely to preserve in asphalt seeps.

Decreasing atmospheric CO_2 concentrations and decreasing sea levels moving the shoreline and coastal moisture sources further away, would have increased environmental stress on LBTP plant communities. These increased environmental stresses may have also played a role in the disappearance of mesic taxa from previous phases.

4.6.5 F5: California Juniper

From ~29.3-25.2 ka *J.* cf. *scopulorum* and *Quercus* are replaced again in the record by *J. californica.* This is roughly coeval to a period of megadrought dating from 27.6-25.7 ka identified in cores from Lake Elsinore and Baldwin Lake (Glover et al., 2020; Heusser et al., 2015; Kirby et al., 2018). While juniper as a genus is relatively drought tolerant, *J. californica* and other serrate leaved junipers are 34-39% more resistant to water-induced xylem cavitation then the sect of junipers *J. scopulorum* belongs to. *J. californica* is physiologically one of the most drought tolerant junipers on the continent (Mahaffey et al., 2020; Willson et al., 2008). Given the physiological differences of the two species, drought is a likely driver behind the replacement of *J. scopulorum* and *Quercus* with *J. californica* at the beginning of MIS 2. There are modern observations of arid juniper-oak woodlands experiencing local die off in response to periods of intense drought (O'Donnell et al., 2020) as well as Holocene transformations from piñon-juniper to oak-juniper woodlands with increasing aridity (Van Devender, 1977).

Sea levels and atmospheric CO_2 continue to decline during this phase. Summer insolation has increased, and winter insolation has remained high. There is a notable dampening of fluctuations in atmospheric temperature and SSTs.

4.6.6 F6: Oak-Juniper Woodland

Phase F5 transitions back into the same oak-juniper woodland from F4 in phase F6. Once again suggesting an open landscape and low-lying herbaceous plant communities. For much of the North American southwest, MIS 2 is generally considered a cooler and wetter period, where a combination of decreased evaporative potential combined with southward shift of the jet stream created large pluvial lakes in what are arid environments today (Oster et al., 2015). In California, pluvial high stands are recorded in the east (Enzel et al., 2003; Koehler & Anderson, 1994; Yang et al., 2005), the San Bernadino Mountains along with increased arboreal pollen (Glover et al., 2017a, 2020; Kirby et al., 2006), and recorded as brief high lake events in Tulare Lake in the Central Valley (Davis, 1999). Pollen and sediment records from Lake Elsinore suggests a cooler, less evaporative LGM that is wetter than the Holocene (Kirby et al., 2018). Marine records off the coast record an increase in pine and Cupressaceae pollen during the glacial maximum (Heusser, 1998, 2000; Heusser & Sirocko, 1997).

It's surprising that LBTP’s pine species disappeared so early in the record, and that the species present in the fossil record for the site are suggestive of a much more arid environment. This phase sees the most stability in atmospheric temperatures and SSTs. Atmospheric CO_2 concentrations and sea levels reach their lowest point in F6, and similar to the majority of *J.* cf. *scopulorum* presence throughout F2, F3, F4, Summer insolation remains relatively low and winter insolation high.

4.6.7 F7: Late-Glacial/Holocene Transition, Woody/Herbaceous

The cluster of *Acer negundo* dates occurring from 16.25-15 ka before the Bølling-Allerød may indicate an increase in precipitation or stream activity. It's lowest annual precipitation within California is 300 mm (based on Calflora observations), lower than the average LGM estimated precipitation. However, today, it is known as a pioneer species in disturbed areas. Since being introduced to Europe in the 17th century it has become one of the most aggressive invasives in riparian environments due to drought tolerance and efficient dispersal via wind and waterways (Sikorska et al., 2019). Lake Elsinore record sand and pollen records indicate a cooler wetter period with increased precipitation from 18.4-14.4 ka connected to Heinrich stadial-1 (HS1) (Kirby et al., 2018).

A large increase in SSTs off the coast is recording from 14.1–12.9 ka and intense upwelling along coastal California during the Bølling (Hendy, 2010). Increasing sea level during this period (Spratt & Lisiecki, 2016) and a closer coastline would have enhanced effects of any coastal fog or low-lying clouds. The uncharacteristically high precipitation estimates at 10 ka may be indicative of a maximum in summer and minimum in winter insolation at LBTP's latitude of 34° N (Laskar et al., 2004).

The preservation of multiple species during F7 may be representative of actual diversity or the product of an increase in specifically woody trees and shrubs, though the preservation of one charred grass seed is notable.

4.6.8 Mid-Holocene Hiatus

The differences in preservation through time (Appendix figure A-6), may have been influenced by temporal variations in seep activity. Increases in temperature moving from glacial periods into the Holocene considered alone, would have acted to increase opportunity for entrapment rather than limiting it. Paucity of plant material in the Holocene may be an artifact of preservation bias between plant communities. Communities like coastal sage scrub are not preserved frequently in the fossil record compared to chaparral, as they're found on steeper hillsides, are lower in height, and have fewer sclerophyllous members with leaves more likely to preserve (Axelrod, 1978). If the area of LBTP shifted towards coastal sage scrub in the Holocene plant material from this period would naturally have limited representation in the seeps compared to other communities. Seed size may also influence long term preservation in asphalt. Average seed size and leaf traits can vary across latitudinal gradients, growth forms, and dispersal strategies (Ackerly, 2003, 2009; Baker, 1972; Moles et al., 2007). Changing environmental conditions may have influenced average seed size and overall preservation rates.

A previous study on LBTP insects has dated a large number of specimens to the Early and Late Holocene, but maintain a similar absence of data from ~10-4 ka in addition to a large gap from 28-16 ka (Holden et al., 2017). This suggests some other factor impacting taphonomic processes and seep activity during the early to mid-Holocene.

4.6.9 F8: 2 ka-Modern

Phase F8 is surprisingly close in species composition to F7 (figure 4-4). The phase begins with a clustered tarweed (*Deinandra fasciculata*) seed dated to 1.9 ka, followed by barley (*Hordeum sp.*) and nightshade (*Solanum parishii*) at 500 CE, followed by the woody taxa of sycamore, boxelder, and elderberry from the modern era. Phases F8 and F7, together, a total reorganization of taxa from the beginning of the record.

4.6.1 Coexistence Analysis

Coexistence analysis of combined species abiotic environmental envelopes suggest annual precipitation as trending downward toward the LGM and up again at the Bølling-Allerød, while temperature estimations remain relatively stable. This pattern of apparent aridity demonstrated by combined species presence may also reflect the influence of decreasing atmospheric CO_2 concentrations on more sensitive taxa as well as the impact of large herds of grazing and browsing megaherbivores on the landscape. Likely it is the product of combined interactions between, climate, CO_2, and fauna.

Inferred precipitation of the coldest quarter, like annual precipitation, trends downward during MIS 2 before rising again after the LGM. During MIS 3 however, combined species estimates of precipitation of the coldest quarter demonstrate large fluctuations in amount of winter precipitation. These fluctuations may be artifacts of sampling gaps. Paleorecords of ODP93 SST and NGRIP atmospheric temperature demonstrated huge variability throughout the floral phases of MIS 3. The peaks of winter precipitation loosely align with the warm SST peaks indicated by the ratio of dextral to sinistral N. Pachyderma from the Santa Barbara Channel (Hendy & Kennett, 2000). Species composition at LBTP might respond to seasonal impacts of increased SST off the coast, though the current level of dating resolution and fossil data is not enough to address this question thoroughly.

The apparent stability of temperature inferred from coexistence analysis of present species suggests a greater importance of moisture availability to temperature for LBTP species composition across the Late Pleistocene and Holocene.

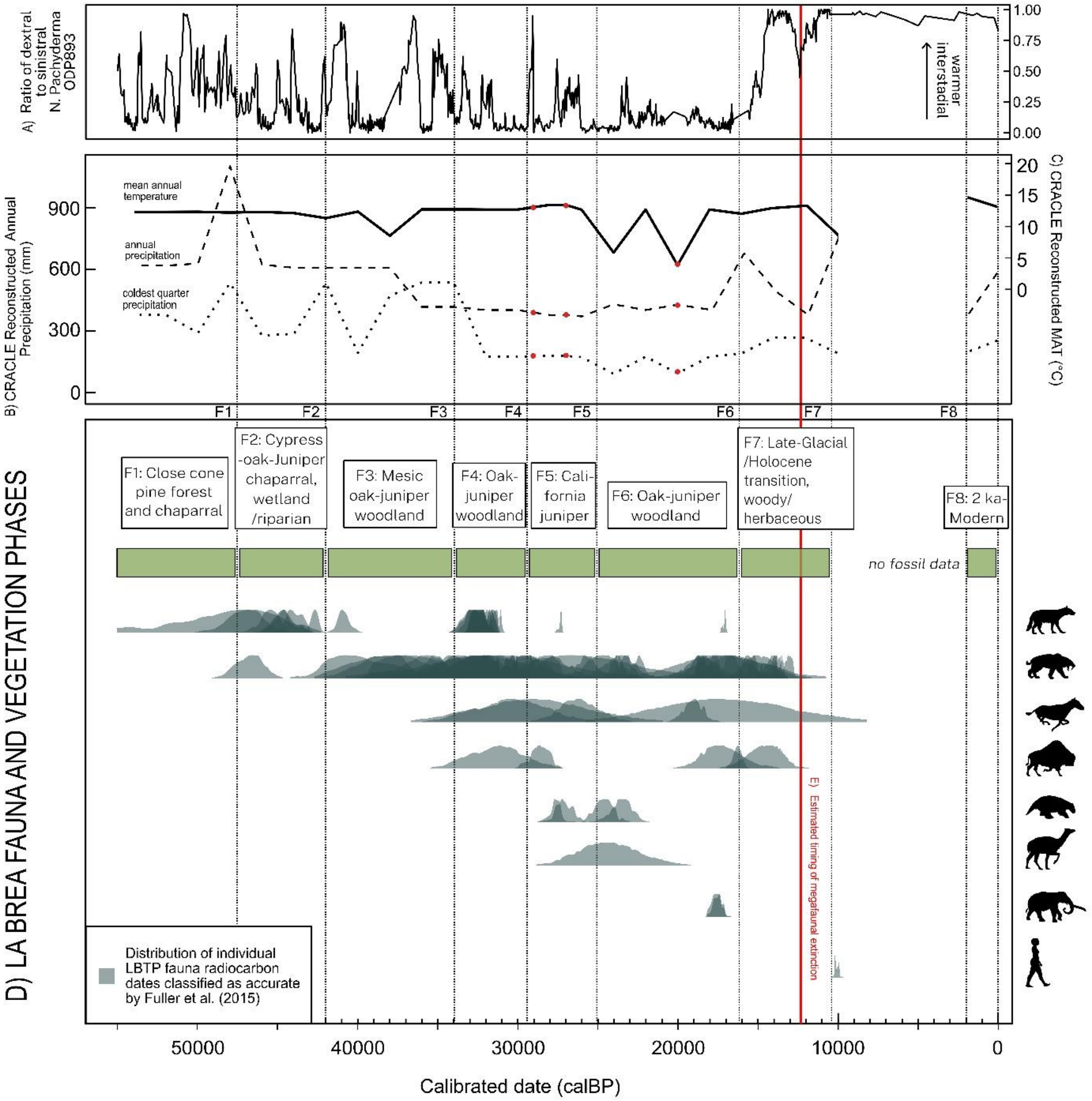


Figure 4-6: Timeline of plant community change plotted against A) Ratio of dextral to sinistral N. pachyderma in Santa Barbara Basin core ODP-893 (Hendy et al. 2007) B-C) CRACLE results for annual precipitation, precipitation in the coldest quarter, and MAT. Red points indicate time slices where only one species is present and value is the mean of California observations D) existing megafauna radiocarbon probability distributions identified as "accurate" from Fuller et al. (2015) calibrated with IntCal20 (Reimer et al. 2020). In order from top: Dire wolf (*Aenocyon dirus*), sabertoothed cat (*Smilodon fatalis*), western horse (*Equus occidentalis*), antique bison (*Bison antiquus*), Harlan's ground sloth (*Paramylodon harlani*), Western camel (*Camelops hesternus*), Columbian mammoth (*Mammuthus* columbi) *and* humans (*Homo sapiens*) *(mammal symbols modified from PhyloPic). Radiocarbon probability distributions are plotted with the estimated extinction date calculated combined plotted megafaunal dates using the Guassian-resampled inverse-weighted McInerny (GRIWM) approach as described in Bradshaw et al. (2012) and Saltré et al. (2015) .*

4.6.2 Megafaunal Interactions

Placing the chronology of plant presences alongside previously dated megafauna reveals interesting correlations. While predators such as the dire wolf (*Aenocyon dirus*) and the saber-toothed cat (*Smilodon fatalis*) exist in what appears to be more closed, forested environments early in the timeline, the herbivorous megafauna are concentrated during the window of more open landscape composed of oak and juniper species. For predator species, this more open habitat seems to favor *S. fatalis* over *A. dirus.*

Studies of this time period on the eastern side of the continent have found the disappearance of megafauna to align closely with the appearance of more woody novel communities of plants, suggesting that these communities are a development of the sudden absence of keystone megafauna rather than a response to climate (Bakker et al., 2016; Gill, 2014, 2014; Gill et al., 2009). The removal of megaherbivores can negatively impact nutrient cycling, plant dispersal, and increase wildfires (Lundgren et al., 2020).

An estimated extinction date calculated with the combined "accurate" megafaunal dates published in Fuller et al., 2015 using the Guassian-resampled inverse-weighted McInerny (GRIWM) approach as described in Bradshaw et al. (2012) and Saltré et al. (2015) produced a median extinction time of 12285.5 ka. The appearance of both *A. negundo* well before this time (16.25 ka) and *S. nigra* by 14.6 ka suggests a reorganization of plant taxa occurring before the extinction of megafauna possibly as a response to increased precipitation connected to HS1.

The extinction of LBTP megafauna occurs within the context of environmental change of the Bølling-Allerød and Younger Dryas. LBTP flora was already exhibiting shifts well before megafaunal disappearance during HS1. However, the reorganization of species during floral phase F7 may both be a response to changes in climate and changes to the population numbers of megaherbivore Grazers and Browsers. Browsers are more likely to consume seedlings of woody species, keeping those populations suppressed. Conversely, juniper populations have historically expanded under year long, high density grazing (Van Auken, 2008).

It's possible that dramatic climate events like the periods of megadrought defined by *J. californica*, were exacerbated by browsing species not allowing drought sensitive taxa to rebound. This would create positive feedback for opening of the landscape and apparent increasing aridity, made worse by low availability of CO_2. A disappearance of large-bodied herbivores and increase in fire at the end of MIS2, would likely negatively impact juniper populations, and contribute to *J.* cf. *scopulorum*'s estimated extinction period of 13-11.7 ka. It would have also prevented *J. californica* from taking its place when conditions became too hot and dry.

4.7 Conclusion

The LBTP flora has shown notable change in composition through time. Those changes largely appear to be responses to orbital changes and variability of Northern Hemisphere atmospheric temperatures and coastal SSTs. Changes to local hydrology appear to be the more direct factor influencing species makeup over temperature, but pressure from interactions with megaherbivores and atmospheric CO_2 concentrations likely also had a role in shaping species composition.

Species composition indicates a shift from higher moisture environments and closed cone pine forest in MIS 3 to a drier climate and more open juniper-oak woodland in MIS 2, punctuated by periods of megadrought indicated by species replacement by *J. californica.* The end of MIS2 and beginning of MIS1 sees the appearance of new broadleaf tree and herbaceous taxa more closely resembling vegetation of the modern period than any other time. It is likely that not all plant communities present at LBTP will preserve equally in the record. Differences in seed traits and growth habits can bias preservation in the seeps. The distinct paucity of data during the Holocene, that may represent a shift to grassland or coastal sage scrub or changes to see activity.

Despite this bias in preservation, the LBTP vegetation record fills an important gap in our understanding of the environmental shifts of the Late Pleistocene and Early Holocene. The chronology illustrates the sensitivity of terrestrial vegetation within the Los Angeles Basin to local and global forcings and provides real examples of species response to a wide range of environmental pressure. This study establishes a baseline of vegetation change for the Los Angeles basin and demonstrated the potential of LBTP flora to address more complex environmental questions in the future.

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Chapter 5 Conclusions

The preserved plant remains from the LBTP are a rich and underutilized resource for data on the vegetation associated with the Rancholabrean mammalian fauna and biological responses to changing climate. This dissertation sought to address this through several approaches. The most prominent conclusions from the resulting taphonomy study of modern seeps, and detailed paleontological study of plant fossils from LBTP collections are outlined below.

The first question of this dissertation, regarding how asphalt seep taphonomic processes influence plant species representation, was addressed in the second chapter. It was concluded that the asphalt seeps are potentially largely hyper-localized in their representation of flora. Seed dispersal mechanisms trapped by seeps are more likely to be gravity, wind, or animal dispersed than water, ruling out seasonal deposition by increased stream flow. The modern seeps studied showed had different vegetation around them and displayed no overlap in plant species captured in the tar despite proximity to one another. Differences in seasonal temperature impact seep flow and subsequently phenologically bias plant species entrapment as well as patterns of faunal interactions.

The second question posed was addressed in the third and fourth chapter. The first part of the question; does flora from LBTP reflect environmental changes in nearby regional records? The overall vegetation assemblages and their chronology, reflected patterns, such as increased conifer presence in the Pleistocene relative to the Holocene, seen in both marine records off the coast of California in the Santa Barbara Basin, Tanner Basin, and Point Conception, as well as lacustrine records in the larger Southern California region, at Baldwin Lake, Lake Tulare, Daimond Valley, and Lake Elsinore. The record appears to show particular affinity to the events recorded in Lake Elsinore, Baldwin Lake and Santa Barbara Basin cores. Shifts in climate and vegetation, often driven by orbital variations, are observed in these records during Marine Isotope Stages (MIS) 3 through 1The second part of that question, do species level records reveal more subtle patterns? We found in chapter three that juniper in the record, although the same genus, post 50 ka, demonstrated remarkable reciprocity in their temporal distribution. It was found likely that periods where *J.* cf. *scopulorum* were replaced by *J. californica* may have been periods of extended drought, most strongly expressed between ~ 27.5 to 25.5 ka, as identified in the Lake Elsinore and Baldwin Lake records. However, the LBTP floral record also yielded some surprises within this general coherence. Most notably, the presence of closed cone pine species at LBTP only occurred during the early portion of MIS3 at ~55 ka to 48 ka. It had been expected that pines might have persisted at LBTP through the Last Glacial Maximum, but this was not the case.

The third question asked if shifts in vegetation related to larger ecological changes with extinction of megafauna and presence of human beings? Again, both chapters three and four addressed this question. Changes in vegetation represented at the LBTP floral record coincide with the changes in mammalian fauna both during MIS 3 and in the transition from MIS 2 and MIS 1. Orbitally driven climatic changes, and high amplitude climatic variability reflecting phenomenon such as the Younger Dryas stadial, clearly played a strong role in the vegetation changes seen at the transition between MIS3 and MIS2, and between MIS2 and MIS1. These changes in vegetation would have impacted the habitat food-web the fauna depended upon and contributed to local presence and extirpation. However, changes in mammalian fauna likely also influenced the flora. The disappearance of large-bodied grazing herbivores and resulting increased fire frequency aided by the sudden influx of herbaceous and woody species and the presence of humans, would have certainly had a large role in the vegetation changes evident in the LBTP flora in the transition from MIS2 to MIS1. This may have contributed to the local extinction of the previously common genus, juniper, at the site. Similarly, the appearance of new species during the Bølling-Allerød would have been a combination of climate and megaherbivore extinction as both browsers and grazers would have had a profound impact on plant species abundance. Combined, this may have contributed to the local extinction of the previously common genus, juniper, at the site.

The patterns of change in plant species presences and local extinctions that are apparent in this reconstructed timeline of vegetation for the Los Angeles Basin provide valuable contextual data to help explain the Rancholabrean Fauna and mega-faunal extinction. The fossil plant record also provides insights for the future of our plant communities today and help us better understand abiotic and biotic tolerances of California native plant species. The observed losses of pines, cypress, and manzanita were influenced by orbital variations, some subtle, that impacted phenomena such as long-term, temperature and hydroclimate trends or shifting patterns of coastal fog. Biotic interactions appear likely to have also to play a role in the presence or absence of key plant species and may be an important factor in a plant community's ability to restore itself after abrupt disruptive events. Vegetation records of the late Quaternary provide some of the closest analogs of modern plant responses to a wide range of abiotic and biotic shifts (Gill, 2014; S. T. Jackson & Williams, 2004). As we see global temperatures rise and precipitation regimes shift in response to anthropogenic climate change (Trenberth et al., 2014), added to the exponential spread of human modified environments (Beltrán et al., 2014; Franklin et al., 2016), fossil plant records are a much-needed supplement to our current understanding of plant community adaptive capacity and general resilience to abrupt and long-term change (Barnosky et al., 2017; S. T. Jackson & Williams, 2004).

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Chapter 6 Appendix

6.1 Chapter 3 Supplemental Tables and Figures

Table A-1: Comparative Descriptions of Juniper Branchlets

	Length of Widest Branchlet (mm) (Eckenwalder 2009)	**Longest Leaf Scale (mm) (Eckenwalder 2009)**	**Leaf Margin (Adams 2014)**	**Leaf Tips (Adams 2014)**	**Leaf Scale Overlap (Adams 2014)**
J. scopulorum	.7-1.5	1-3	entire	obtuse-acute	<1/5
J. maritima	1.1-1.5	>1.5	entire	obtuse	<1/5
J. horizontalis	1.1-1.5	>1.5	entire	apiculate	mostly overlapping
J. blancoi	<1	1.5-2	entire	acuminate with obtuse to acute apressed tips	
J. virginiana	1.1-1.3	1-3	entire	acute	>1/4
Fossil Juniper	1.07-1.65 (1.38 mean)	1.24-2.15 (1.52 mean)	entire	obtuse-acute	<1/5

Table A-2: ImageJ Juniper Measurements for PCA

	Area	*Perimeter*	*Major*	*Minor*	*Round*	*Solidity*	*Basal Min/Max Feret Ratio*	*Basal Aspect Ratio*
J. blancoi	7.358	10.735	3.417	2.742	0.802	0.984	0.877535	1.139
J. blancoi	5.724	9.968	3.501	2.082	0.595	0.984	0.948808	1.054
J. blancoi	6.141	10.802	3.387	2.309	0.682	0.965	0.916352	1.091
J. blancoi	8.91	12.105	4.082	2.779	0.681	0.984	0.840403	1.19
J. blancoi	8.929	12.078	4.062	2.799	0.689	0.986	0.819054	1.221
J. blancoi	7.435	11.055	3.952	2.395	0.606	0.981	0.855696	1.168
J. blancoi	6.111	10.97	3.986	1.952	0.49	0.98	0.854395	1.17
J. blancoi	8.914	11.994	4.012	2.829	0.705	0.988	0.86843	1.151
J. blancoi	7.529	11.662	4.12	2.327	0.565	0.979	0.860132	1.162
J. virginiana	5.243	9.064	3.047	2.191	0.719	0.969	0.894671	1.118
J. virginiana	5.497	9.154	2.985	2.344	0.785	0.964	0.837892	1.193

J. virginiana	5.625	9.136	3.093	2.315	0.748	0.971	0.715235	1.398
J. virginiana	5.193	8.845	2.84	2.328	0.82	0.969	0.808845	1.236
J. virginiana	6.258	9.977	3.536	2.253	0.637	0.972	0.827465	1.208
J. virginiana	5.587	9.067	2.925	2.432	0.831	0.968	0.931466	1.073
J. virginiana	5.949	9.388	3.038	2.494	0.821	0.967	0.675121	1.481
J. virginiana	4.768	8.42	2.747	2.21	0.805	0.97	0.66941	1.493
J. virginiana	5.299	9.087	3.06	2.205	0.721	0.963	0.87284	1.146
J. virginiana	3.862	7.578	2.577	1.908	0.741	0.972	0.837156	1.194
J. virginiana	4.681	8.351	2.759	2.161	0.783	0.971	0.690508	1.448
J. virginiana	4.422	8.09	2.593	2.171	0.837	0.969	0.654117	1.528
J. virginiana	4.58	8.125	2.698	2.161	0.801	0.97	0.878284	1.139
J. virginiana	4.953	8.82	3.189	1.977	0.62	0.972	0.693996	1.441
J. virginiana	4.271	7.93	2.619	2.076	0.793	0.965	0.772171	1.295
J. virginiana	4.246	7.94	2.574	2.1	0.816	0.966	0.867249	1.153
J. virginiana	6.048	9.601	3.288	2.342	0.712	0.971	0.839705	1.191
J. virginiana	6.068	9.633	3.097	2.495	0.806	0.956	0.730247	1.369
J. virginiana	4.268	7.889	2.614	2.079	0.795	0.975	0.866924	1.153
J. virginiana	4.804	8.463	2.795	2.188	0.783	0.966	0.802945	1.246
J. virginiana	5.067	8.626	2.833	2.278	0.804	0.971	0.936508	1.068
J. virginiana	4.736	8.362	2.831	2.13	0.752	0.973	0.900727	1.11
J. virginiana	4.839	8.523	2.925	2.107	0.72	0.971	0.772	1.296
J. virginiana	5.287	8.841	2.879	2.338	0.812	0.973	0.862245	1.159
J. virginiana	4.594	8.238	2.881	2.03	0.705	0.975	0.943035	1.061
J. virginiana	5.739	9.171	3.076	2.375	0.772	0.973	0.642582	1.556

J. virginiana	5.033	8.834	2.99	2.144	0.717	0.97	0.890152	1.124
J. virginiana	3.682	7.513	2.567	1.826	0.712	0.964	0.892193	1.121
J. virginiana	6.652	10.249	3.45	2.455	0.712	0.966	0.942116	1.062
J. virginiana	5.536	9.097	3.098	2.275	0.734	0.977	0.794957	1.258
J. virginiana	4.657	9.117	3.304	1.794	0.543	0.962	0.70532	1.418
J. virginiana	5.529	9.185	3.014	2.336	0.775	0.965	0.752467	1.329
J. virginiana	4.852	8.547	2.792	2.213	0.792	0.971	0.873475	1.145
J. virginiana	3.581	7.434	2.472	1.844	0.746	0.961	0.774829	1.291
J. virginiana	5.01	8.625	2.94	2.17	0.738	0.972	0.834251	1.199
J. virginiana	4.32	8.476	3.083	1.784	0.579	0.958	0.840252	1.191
J. virginiana	5.841	9.351	3.081	2.414	0.783	0.971	0.886792	1.128
J. virginiana	4.623	8.517	3.055	1.927	0.631	0.973	0.906311	1.103
J. virginiana	4.578	8.774	3.159	1.845	0.584	0.963	0.849955	1.177
J. virginiana	5.035	8.634	2.969	2.159	0.727	0.976	0.751012	1.331
J. virginiana	5.204	8.93	3.131	2.117	0.676	0.966	0.813231	1.23
J. virginiana	6.13	9.863	3.479	2.243	0.645	0.971	0.954854	1.047
J. virginiana	5.086	8.898	3.085	2.099	0.68	0.966	0.86326	1.158
J. virginiana	3.905	7.629	2.534	1.962	0.775	0.969	0.855229	1.169
J. virginiana	5.843	9.486	3.348	2.222	0.664	0.974	0.725855	1.377
J. virginiana	5.09	8.671	2.849	2.275	0.799	0.968	0.856385	1.168
J. virginiana	5.359	9.11	3.078	2.217	0.72	0.968	0.660971	1.512
J. virginiana	4.19	7.958	2.765	1.93	0.698	0.966	0.711606	1.405
J. virginiana	5.077	8.993	3.176	2.036	0.641	0.959	0.894519	1.118
J. virginiana	5.887	9.841	3.478	2.155	0.62	0.964	0.862809	1.159

J. virginiana	4.086	7.922	2.692	1.933	0.718	0.966	0.946533	1.057
J. virginiana	4.762	8.612	3.025	2.004	0.663	0.97	0.934346	1.071
J. virginiana	6.439	9.939	3.551	2.309	0.65	0.972	0.958597	1.043
J. virginiana	4.881	8.503	2.784	2.232	0.802	0.973	0.789036	1.267
J. virginiana	5.116	8.818	2.998	2.173	0.725	0.966	0.61394	1.629
J. virginiana	4.656	8.397	2.857	2.075	0.726	0.968	0.853131	1.172
J. virginiana	4.757	8.56	3.047	1.988	0.652	0.977	0.75384	1.327
J. virginiana	5.096	9.055	3.215	2.018	0.628	0.971	0.794233	1.259
J. virginiana	4.93	8.891	3.019	2.079	0.689	0.961	0.84282	1.186
J. virginiana	4.229	8.145	2.84	1.896	0.668	0.97	0.745508	1.342
J. virginiana	5.462	9.049	2.958	2.351	0.795	0.967	0.93126	1.074
J. virginiana	5.133	8.978	3.141	2.08	0.662	0.971	0.957952	1.044
J. virginiana	4.665	8.811	3.221	1.844	0.573	0.962	0.869167	1.151
J. virginiana	3.209	7.044	2.354	1.736	0.737	0.964	0.840982	1.189
J. scopulorum	6.949	10.164	3.29	2.69	0.818	0.967	0.719068	1.391
J. scopulorum	6.194	9.521	3.022	2.61	0.864	0.97	0.78526	1.273
J. scopulorum	7.031	10.291	3.16	2.833	0.897	0.971	0.748464	1.336
J. scopulorum	7.314	10.399	3.068	3.036	0.989	0.972	0.819718	1.22
J. scopulorum	6.496	9.816	3.127	2.645	0.846	0.972	0.637161	1.569
J. scopulorum	5.524	9.068	3.146	2.236	0.711	0.971	0.831453	1.203
J. scopulorum	9.784	12.118	3.961	3.145	0.794	0.974	0.820935	1.218
J. scopulorum	7.2	10.339	3.33	2.753	0.827	0.968	0.804514	1.243
J. scopulorum	10.046	12.217	4.064	3.148	0.775	0.977	0.714109	1.401
J. scopulorum	8.877	11.446	3.629	3.115	0.858	0.971	0.763433	1.31

J. scopulorum	6.606	10.221	3.471	2.423	0.698	0.966	0.700212	1.428
J. scopulorum	7.979	10.927	3.641	2.79	0.766	0.972	0.978998	1.021
J. scopulorum	7.671	10.794	3.496	2.794	0.799	0.97	0.749914	1.333
J. scopulorum	10.241	12.293	4.038	3.23	0.8	0.974	0.798771	1.252
J. scopulorum	10.265	12.295	3.838	3.406	0.887	0.976	0.816229	1.225
J. scopulorum	8.579	11.099	3.401	3.211	0.944	0.973	0.656693	1.523
J. scopulorum	10.102	12.764	4.569	2.815	0.616	0.97	0.789025	1.267
J. scopulorum	11.667	13.455	4.105	3.619	0.881	0.966	0.821839	1.217
J. scopulorum	7.426	10.478	3.155	2.996	0.95	0.969	0.688316	1.453
J. scopulorum	6.379	10.116	3.53	2.301	0.652	0.964	0.780501	1.281
J. scopulorum	8.041	11.459	4.074	2.513	0.617	0.966	0.792412	1.262
J. scopulorum	7.311	10.693	3.787	2.458	0.649	0.966	0.702948	1.423
J. scopulorum	5.49	9.441	3.423	2.042	0.597	0.967	0.7827	1.278
J. scopulorum	10.164	12.242	3.763	3.439	0.914	0.967	0.751498	1.331
J. scopulorum	8.286	11.276	3.86	2.733	0.708	0.969	0.853399	1.172
J. scopulorum	8.114	11.274	3.738	2.764	0.739	0.966	0.840415	1.19
J. scopulorum	6.698	10.45	3.536	2.412	0.682	0.958	0.647756	1.543
J. scopulorum	7.301	10.478	3.222	2.885	0.895	0.966	0.696478	1.436
J. scopulorum	6.883	10.734	3.805	2.303	0.605	0.963	0.939503	1.064
J. scopulorum	6.035	9.611	3.315	2.318	0.699	0.975	0.792939	1.261
J. scopulorum	9.559	11.88	3.598	3.383	0.94	0.97	0.548326	1.824
J. scopulorum	6.675	9.984	3.445	2.467	0.716	0.975	0.804724	1.242
J. scopulorum	8.499	11.358	3.868	2.798	0.723	0.969	0.81196	1.232
J. scopulorum	6.001	9.997	3.703	2.063	0.557	0.962	0.954281	1.048

J. scopulorum	7.928	11.277	4.018	2.512	0.625	0.968	0.785507	1.273
J. scopulorum	8.372	11.785	4.223	2.524	0.598	0.968	0.679516	1.471
J. scopulorum	9.687	12.549	4.569	2.699	0.591	0.971	0.887299	1.127
J. scopulorum	7.08	10.804	3.822	2.358	0.617	0.964	0.861224	1.161
J. scopulorum	4.934	8.613	2.91	2.159	0.742	0.967	0.839766	1.191
J. scopulorum	7.66	10.784	3.612	2.7	0.748	0.967	0.849627	1.177
J. scopulorum	8.463	12.281	4.571	2.357	0.516	0.961	0.873844	1.144
J. scopulorum	4.712	8.775	3.186	1.883	0.591	0.969	0.737582	1.355
J. scopulorum	6.284	9.86	3.473	2.304	0.663	0.968	0.895625	1.116
J. scopulorum	5.245	9.35	3.382	1.974	0.584	0.951	0.956276	1.046
J. scopulorum	6.346	9.942	3.398	2.378	0.7	0.968	0.673107	1.485
J. scopulorum	7.436	11.158	3.725	2.542	0.682	0.987	0.954698	1.048
J. scopulorum	7.077	11.212	3.848	2.342	0.609	0.984	0.690956	1.447
J. scopulorum	6.654	10.616	3.597	2.355	0.655	0.989	0.863079	1.158
J. scopulorum	5.92	9.751	3.13	2.408	0.77	0.981	0.658462	1.519
J. scopulorum	7.306	10.906	3.514	2.647	0.753	0.987	0.842219	1.188
J. scopulorum	6.422	10.331	3.386	2.415	0.713	0.981	0.907679	1.101
J. scopulorum	5.526	9.363	2.954	2.382	0.806	0.984	0.859649	1.163
J. scopulorum	5.684	9.367	2.955	2.449	0.829	0.99	0.706288	1.415
fossil juniper	7.127	11.777	3.593	2.525	0.703	0.973	0.769391	1.3
fossil juniper	6.837	10.704	3.312	2.629	0.794	0.986	0.817773	1.223
fossil juniper	7.099	10.906	3.256	2.777	0.853	0.987	0.813438	1.229
fossil juniper	5.941	10.209	3.131	2.416	0.771	0.984	0.946967	1.056
fossil juniper	7.836	11.969	3.647	2.736	0.75	0.987	0.803842	1.244

fossil juniper	6.079	10.016	3.233	2.394	0.741	0.99	0.671518	1.489
fossil juniper	7.003	11.152	3.571	2.497	0.699	0.96	0.894915	1.117
fossil juniper	9.089	12.552	4.012	2.885	0.719	0.987	0.757613	1.32
fossil juniper	5.682	9.971	3	2.412	0.804	0.971	0.95604	1.046
fossil juniper	7.436	11.158	3.725	2.542	0.682	0.987	0.954698	1.048
fossil juniper	7.077	11.212	3.848	2.342	0.609	0.984	0.690956	1.447
fossil juniper	6.654	10.616	3.597	2.355	0.655	0.989	0.863079	1.158
fossil juniper	5.92	9.751	3.13	2.408	0.77	0.981	0.658462	1.519
fossil juniper	7.306	10.906	3.514	2.647	0.753	0.987	0.842219	1.188
fossil juniper	6.422	10.331	3.386	2.415	0.713	0.981	0.907679	1.101
fossil juniper	5.526	9.363	2.954	2.382	0.806	0.984	0.859649	1.163
fossil juniper	5.684	9.367	2.955	2.449	0.829	0.99	0.706288	1.415

Table A-3: CT Measurements of Juniper

species	**seed volume (mm3)**	**max feret (mm)**	**surface area (mm2)**	**micropyle ratio**	**micropyle width**	**mean feret (mm)**	**integument vol (mm3)**	**negative convex hull ratio**	**negative capsule ratio**
Fossil	9.96	3.56	27.21	20	0.01	3.23	6.48	88.37622	0.525714
Fossil	9.13	3.84	24.73	13.5	0.02	2.94	6.29	90.30663	0.47619
Fossil	6.52	3.14	20.93	9	0.01	2.79	4.24	84.12903	0.507553
Fossil	6.82	3.21	23.27	12	0.01	2.76	5.31	89.85507	0.495562
Fossil	6.49	2.92	19	18	0.01	2.61	5.22	93.38129	0.445299
J. blancoi	8.96	3.95	27.05	5	0.03	3.34	4.08	89.24303	0.5625

J. blancoi	9.31	4.13	25.92	9.5	0.02	3.39	4.78	88.33017	0.490142
J. blancoi	11.08	4.23	41.18	7	0.01	3.46	5.72	84.3869	0.528711
J. blancoi	8.33	3.3	22.16	8	0.02	2.76	4.58	85.4359	0.46534
J. blancoi	7.64	3.71	30.24	6.5	0.02	3.25	4.61	82.4164	0.585233
J. scopulorum	14.54	4.24	35.82	4	0.03	3.76	9.58	83.61127	0.470117
J. scopulorum	12.53	3.97	29.26	6.5	0.04	3.54	7.43	93.71728	0.423643
J. scopulorum	5.09	3.41	16.34	7.5	0.02	2.72	2.3	94.60967	0.483249
J. scopulorum	6.28	3.47	19.11	6	0.03	2.94	3.36	93.45238	0.540936
J. scopulorum	5.71	3.14	18.52	7.333333	0.03	2.64	3.28	92.09677	0.507759
J. virg. E	8.71	3.5	23.37	4.25	0.04	3.08	6.21	92.95624	0.474034
J. virg. E	7.58	3.63	22.4	8.666667	0.03	3.18	5.7	93.81188	0.426626
J. virg. E	5.5	2.98	17.12	4.2	0.05	2.6	3.46	94.82759	0.455446
J. virg. E	4.38	2.79	15.32	4	0.05	2.44	2.23	94.19355	0.447667
J. virg. E	3.83	2.69	13.4	5.5	0.04	2.13	1.91	91.84652	0.435103
J. virg. Mid	6.17	3.5	20.02	12.5	0.02	2.9	3.53	94.6319	0.511867
J. virg. Mid	6.13	3.95	18.52	17	0.01	3.34	2.64	88.84058	0.505645
J. virg. Mid	12.74	3.73	30.34	8.5	0.02	3.26	7.04	88.10512	0.388676
J. virg. Mid	6.68	3.37	20.57	10.5	0.02	2.88	3.46	93.55742	0.482171
J. virg. Mid	6.19	3.59	18.8	25	0.01	2.9	3.62	95.08449	0.533183

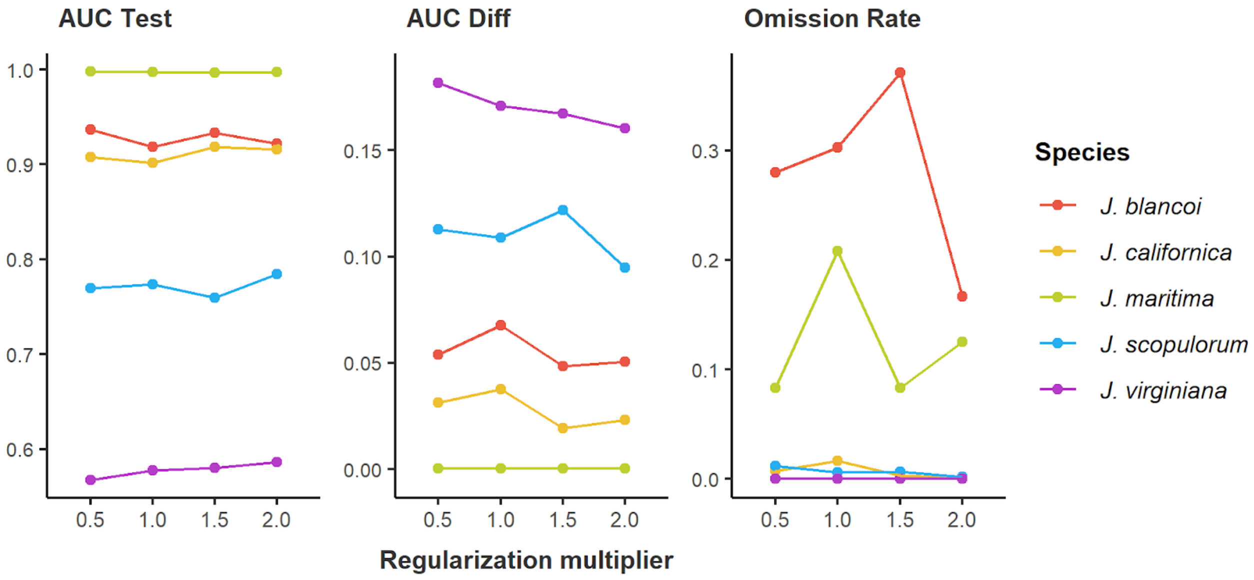

Figure A-1: Evaluation metrics for four regularization multipliers tested in modeling juniper species: test AUC (AUC$_{Test}$), difference between test and training AUC (AUC$_{Diff}$), and omission rate using the minimum training presence threshold. Relatively higher AUC$_{Test}$ and lower AUC$_{Diff}$ and omission rates indicate better model performance.

Table A-4: Sample sizes and regularization (reg.) multiplier used in the final model for each juniper species. The latter was selected based on metrics averaged from cross-validated models: test AUC (AUC$_{Test}$), difference between test and training AUC (AUC$_{Diff}$), and omission rate using the minimum training presence threshold (MTP). Relatively higher AUC$_{Test}$ and lower AUC$_{Diff}$ and omission rates indicate better model performance.

		Cross-validation results			
Species	Sample size[1]	Regularization multiplier	AUC$_{Test}$	AUC$_{Diff}$	MTP omission rate
J. blancoi	38	2.0	0.922 ±0.071	0.051 ±0.081	0.167 ±0.333
J. californica	1656	1.5	0.919 ±0.007	0.019 ±0.009	0.003 ±0.004
J. maritima	25	0.5	0.998 ±0.001	0.001 ±0.001	0.083 ±0.096
J. scopulorum	2148	2.0	0.784 ±0.073	0.095 ±0.08	0.002 ±0.003
J. virginiana	11090	2.0	0.587 ±0.11	0.16 ±0.111	0.0002 ±0.0004

[1] Duplicates removed.

Table A-5: AMS radiocarbon dates of individual fossil Juniperus seeds.

Collection #	UCIAMS #	Taxon	Fraction	±	d^{14}C (‰)	±	14C age	±
HC 696B	216493	*J. californica*	0.0617	0.0006	-938.3	0.6	22370	80
HC 697B	216494	*J. californica*	0.0020	0.0005	-998.0	0.5	50000	2100
HC 699B	216495	*J. californica*	0.0009	0.0005	-999.1	0.5	>50300	
HC 700B	216496	*J. californica*	0.0006	0.0005	-999.4	0.5	>49200	
HC 705B	216502	*J. californica*	0.0009	0.0005	-999.1	0.5	>50300	
HC 706B	216503	*J. californica*	0.0010	0.0005	-999.0	0.5	>44600	
HC 707B	216504	*J. californica*	0.0625	0.0006	-937.5	0.6	22270	80
RLP 718B	216514	*J. californica*	0.0493	0.0006	-950.7	0.6	24180	100
HC 729B	218582	*J. californica*	0.0730	0.0004	-927.0	0.4	21025	50
HC 730B	218583	*J. californica*	0.0714	0.0004	-928.6	0.4	21200	60
HC 734B	218585	*J. californica*	0.0002	0.0003	-999.8	0.3	>57300	
HC 574B	198384	*J. californica*	0.0008	0.0005	-999.2	0.5	>50800	
HC 577B	198387	*J. californica*	0.0016	0.0005	-998.4	0.5	51800	2500
HC 686B	212954	*J. californica*	0.0639	0.0006	-936.1	0.6	22090	80
HC 687B	212955	*J. californica*	0.0004	0.0006	-999.6	0.6	>51600	
HC 688B	212956	*J. californica*	0.0002	0.0006	-999.8	0.6	>52700	
RLP 436B	252126	*J. californica*	0.0703	0.0006	-929.7	0.6	21330	80
RLP 1442B	252174	*J. californica*	0.0009	0.0005	-999.1	0.5	>50300	
RLP 1468B	252175	*J. californica*	0.0009	0.0005	-999.1	0.5	>50300	
RLP 533B	193854	*J. californica*	0.0046	0.0005	-995.4	0.5	43230	940
RLP 534B	193855	*J. californica*	0.0452	0.0006	-954.8	0.6	24870	110
RLP 539B	193860	*J. californica*	0.0710	0.0006	-929.0	0.6	21250	70
HC 691B	216488	*J.* cf. *scopulorum*	0.0922	0.0006	-907.8	0.6	19150	60
HC 692B	216489	*J.* cf. *scopulorum*	0.0946	0.0006	-905.4	0.6	18940	60
HC 693B	*216490*	*J.* cf. *scopulorum*	0.04044	0.00056	-959.56	0.55606	25770	120
HC 694B	216491	*J.* cf. *scopulorum*	0.0380	0.0006	-962.0	0.6	26270	130
HC 695B	216492	*J.* cf. *scopulorum*	0.0740	0.0006	-926.0	0.6	20920	70

HC 708B	216505	*J.* cf. *scopulorum*	0.0008	0.0005	-999.2	0.5	>50800	
HC 709B	216506	*J.* cf. *scopulorum*	0.0018	0.0005	-998.2	0.5	50700	2300
HC 710B	216507	*J.* cf. *scopulorum*	0.0123	0.0051	-987.7	5.1	35300	3300
HC 711B	216508	*J.* cf. *scopulorum*	0.0014	0.0005	-998.6	0.5	52500	2900
HC 712B	216509	*J.* cf. *scopulorum*	0.1805	0.0008	-819.5	0.8	13750	40
HC 713B	216510	*J.* cf. *scopulorum*	0.0022	0.0020	-997.8	2.0	>40800	
HC 745B	218589	*J.* cf. *scopulorum*	0.0154	0.0004	-984.6	0.4	33510	200
HC 746B	218590	*J.* cf. *scopulorum*	0.0156	0.0004	-984.4	0.4	33450	200
HC 748B	218596	*J.* cf. *scopulorum*	0.0221	0.0004	-977.9	0.4	30640	160
HC 749B	218597	*J.* cf. *scopulorum*	0.0279	0.0004	-972.1	0.4	28760	120
HC 750B	218598	*J.* cf. *scopulorum*	0.0270	0.0004	-973.0	0.4	29000	120
HC 575B	198385	*J.* cf. *scopulorum*	0.0316	0.0006	-968.4	0.6	27740	150
HC 576B	198386	*J.* cf. *scopulorum*	0.2040	0.0008	-796.0	0.8	12770	35
HC 674B	212951	*J.* cf. *scopulorum*	0.0147	0.0006	-985.3	0.6	33890	350
HC 684B	212952	*J.* cf. *scopulorum*	0.0011	0.0006	-998.9	0.6	>48500	
HC 685B	212953	*J.* cf. *scopulorum*	0.0263	0.0006	-973.7	0.6	29240	200
RLP 683B	252127	*J.* cf. *scopulorum*	0.0217	0.0006	-978.3	0.6	30770	220
HC 757B	252129	*J.* cf. *scopulorum*	0.0025	0.0006	-997.5	0.6	48300	2100
RLP 763B	252130	*J.* cf. *scopulorum*	0.1308	0.0008	-869.2	0.8	16335	50
RLP 782B	252131	*J.* cf. *scopulorum*	0.0013	0.0006	-998.7	0.6	53700	4000
RLP 1005B	252139	*J.* cf. *scopulorum*	0.0365	0.0006	-963.5	0.6	26600	140
RLP 1016B	252140	*J.* cf. *scopulorum*	0.1609	0.0007	-839.1	0.7	14675	40

RLP 1022B	252142	*J.* cf. *scopulorum*	0.0782	0.0006	-921.8	0.6	20470	70
RLP 1053B	252148	*J.* cf. *scopulorum*	0.0372	0.0006	-962.8	0.6	26430	130
RLP 1080B	252168	*J.* cf. *scopulorum*	0.0375	0.0005	-962.5	0.5	26370	120
RLP 1082B	252170	*J.* cf. *scopulorum*	0.1013	0.0008	-898.7	0.8	18390	70
RLP 1083B	252171	*J.* cf. *scopulorum*	0.0784	0.0007	-921.6	0.7	20450	80
RLP 553B	193873	*J.* cf. *scopulorum*	0.0156	0.0005	-984.4	0.5	33440	280
RLP 561B	193881	J. cf. *scopulorum*	0.0010	0.0005	-999.0	0.5	>49900	

6.2 Chapter 4 Supplemental Tables and Figures

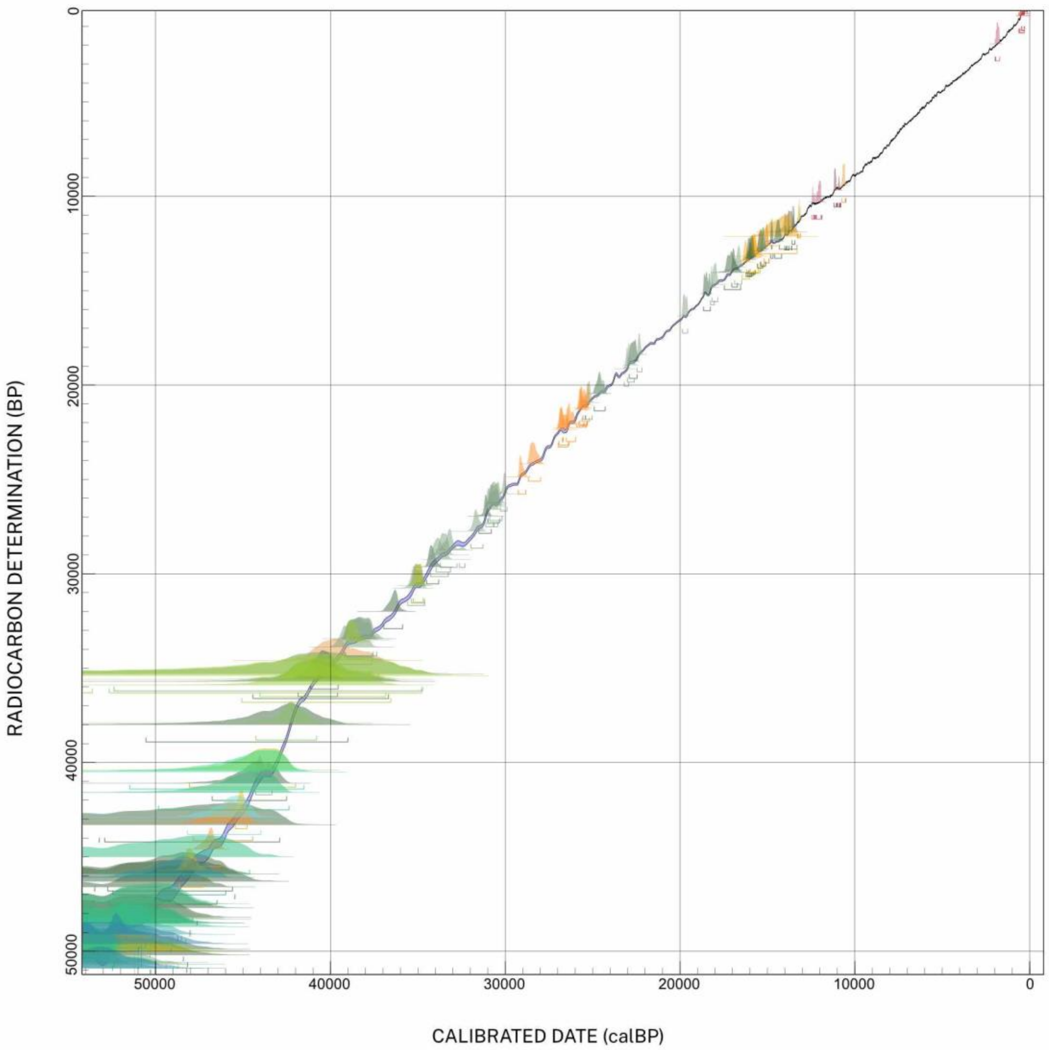

Figure A-2: AMS radiocarbon dates of flora plotted along calibration curve with a clear absence of dates during the Holocene ~10.7-2 ka. Colors reflect taxa coloration in figure 4-3.

Table A-6: Specimen list for AMS radiocarbon dates

RLB Collection #:	**UCIAMS #**	**Element:**	**Deposit:**	**Grid:**	**fraction**	**±**	**$d^{14}C$ (‰)**	**±**	**^{14}C age**	**±**
Water parsley (O*enanthe sarmentosa* C. Presl ex DC., Apiales: Apiaceae)										
RLP 1067B	252152	fruit	Pit 91	GJM	0.0121	0.0060	-987.9	6.0	35400	4000
RLP 724B	218579	fruit	Pit 91	GJM 584/5-7	0.0114	0.0028	-988.6	2.8	35900	2000
RLP 725B	218580	2 fruits	Pit 91	GJM 584/5-7	0.0119	0.0027	-988.1	2.7	35600	1800
RLP 571B	198382	fruit	Pit 91	GJM 584/F-7	0.0020	0.0007	-998.0	0.7	50000	2800
Baccharis (*Baccharis sp.*, Asterales: Asteraceae: Asteroideae: Astereae)										
RLP 1069B	252156	2 achenes	Pit 91	GJM	1.4178	0.0048	417.8	4.8	MODERN	
RLP 1077B	252164	2 achenes	Pit 91	GJM	1.3969	0.0112	396.9	11.2	MODERN	
Deltoid balsam root (*Balsamorhiza deltoidei* Nutt., Asterales: Asteraceae)										
RLP 568B	198379	1 achene	Pit 91	GJM 596/F-6	0.0066	0.0014	-993.4	1.4	40400	1700
RLP 1079B	252167	1 achene	Pit 91	GJM	0.0089	0.0066	-991.1	6.6	>30600	
Clustered tarweed (*Deinandra fasciculata* (DC.) Greene, Asterales: Asteraceae: Asteroideae: Madieae)										
RLP 1070B	252157	achene	Pit 91	GJM	0.9794	0.0023	-20.6	2.3	165	20
RLP 1076B	252163	achene	Pit 91	GJM	0.2773	0.0011	-722.7	1.1	10305	35
RLP 567B	198378	achene	Pit 91	GJM 288/M-9	0.7872	0.0014	-212.8	1.4	1920	15
Common madia (*Madia elegans* D. Don, Asterales: Asteraceae)										

RLP 1074B	252161	1 achene	Pit 91	GJM	0.2275	0.0055	-772.5	5.5	11890	200
Saltbush (*Atriplex* sp., Caryophyllales: Chenopodiaceae: Chenopodioideae)										
RLP 1073B	252160	1 achene	Pit 91	GJM	0.2209	0.0103	-779.1	10.3	12130	380
American dogwood (*Cornus sericea* L., Cornales: Cornaceae)										
HC 564B	198375	endocarp	Pit 101		0.0013	0.0005	-998.7	0.5	53700	3100
HC 704B	216498	endocarp	Pit A		0.0048	0.0006	-995.2	0.6	42900	1100
Blue elderberry (*Sambucus mexicana* C. Presl ex DC., Dipsacales: Viburnaceae)										
RLP 1075B	252162	endocarp	Pit 91	GJM	0.2124	0.0036	-787.6	3.6	12450	140
RLP 720B	218576	3 endocarps	Pit 91	GJM 295/M-3	1.3657	0.0030	365.7	3.0	MODERN	
HC 565B	198376	endocarp	Pit 3		0.0135	0.0017	-986.5	1.7	34600	1000
RLP 570B	198381	endocarp	Pit 91	GJM 295/M-5	0.3098	0.0014	-690.2	1.4	9415	40
Big berry manzanita (*Arctostaphylos glauca* Lindl., Ericales: Ericaceae: Arbutoideae)										
RLP 544B	193865	fragment of fused nutlets	Pit91	RLP 923/E-7	-0.0001	-0.0005	-1000.1	-0.5	>55500	
RLP 545B	193866	fragment of fused nutlets	Pit91	RLP 923/E-7	0.0000	-0.0005	-1000.0	-0.5	>55500	
RLP 546B	193867	fragment of fused nutlets	Pit91	RLP 923/E-7	0.0065	0.0018	-993.5	1.8	40500	2200
Manzanita (*Arctostaphylos* sp., Ericales: Ericaceae: Arbutoideae)										
HC 735B	218586	1 nutlet	Pit 13		0.0022	0.0005	-997.8	0.5	49100	1700
HC 738B	218587	1 nutlet	Pit A		0.0012	0.0006	-998.8	0.6	>48500	

Coast live oak (*Quercus agrifolia* Née, Fagales: Fagaceae)										
RLP 761B	224291	leaf	Pit 91	GJM 273/N-3	0.2008	0.0007	-799.2	0.7	12895	30
RLP 768B	224294	leaf	Pit 91	GJM 273/N-3	0.1896	0.0008	-810.4	0.8	13355	35
HC 786B	224295	cupule	Pit 3		0.0089	0.0025	-991.1	2.5	38000	2300
HC 787B	224296	cupule	Pit 3		0.0016	0.0006	-998.4	0.6	51800	3200
HC 788B	224297	acorn	Pit 3		0.0019	0.0008	-998.1	0.8	50200	3500
HC 789B	224298	acorn	Pit 3		0.0045	0.0022	-995.5	2.2	43300	3900
HC 794B	224299	acorn	Pit A		0.0030	0.0005	-997.0	0.5	46600	1400
HC 802B	224309	acorn	Pit A		0.0012	0.0006	-998.8	0.6	>48500	
HC 742B	218588	cupule	Pit 4		0.1910	0.0009	-809.0	0.9	13300	40
RLP 537B	193858	cupule	Pit91	GJM372+373/L-9+L-8	0.0250	0.0005	-975.0	0.5	29630	180
RLP 538B	193859	cupule	Pit91	GJM 401/L-3	0.2261	0.0007	-773.9	0.7	11945	25
RLP 547B	193868	cupule	Pit91	RLP 923/E-7	0.0005	0.0005	-999.5	0.5	>52200	
RLP 560B	193880	cupule	Pit 4		0.0026	0.0006	-997.4	0.6	47700	1900
RLP 766B	224293	cupule	Pit 91	GJM 408/L-4	0.2034	0.0007	-796.6	0.7	12790	30
HC 795B	224300	acorn	Pit 4		0.1515	0.0010	-848.5	1.0	15160	60
HC 797B	224307	cup	Pit A		0.0117	0.0028	-988.3	2.8	35700	1900
HC 799B	224308	acorn	Pit 3		0.1772	0.0007	-822.8	0.7	13900	35
HC 806B	224310	acorn	Pit A		0.0060	0.0009	-994.0	0.9	41100	1300
HC 807B	224311	cupule	Pit A		0.0125	0.0006	-987.5	0.6	35200	410

HC 810B	224312	cupule	Pit A		0.0020	0.0008	-998.0	0.8	49900	3300
HC 811B	224313	cupule	Pit A		0.0007	0.0006	-999.3	0.6	>50300	
HC 816B	224314	cupule	Pit 3		0.0033	0.0007	-996.7	0.7	45900	1800
Nutall’s scrub oak (*Quercus* cf. *dumosa*, Fagales: Fagaceae)										
RLP 715B	216512	gall	Pit 91	GJM 401/L-3	0.2346	0.0010	-765.4	1.0	11645	40
RLP 717B	216513	gall	Pit 93	GJM 401/L-3	0.2143	0.0009	-785.7	0.9	12375	35
Oak (*Quercus* sp., Fagales: Fagaceae)										
HC 731B	252128	leaf	LACM 1814		-0.0002	-0.0006	-1000.2	-0.6	>54000	
HC 796B	252132	leaf	Pit 4		0.1925	0.0012	-807.5	1.2	13235	50
HC 798B	252135	leaf	Pit A		0.0031	0.0013	-996.9	1.3	46300	3200
HC 800B	252136	leaf	Pit 3	C-4	0.1742	0.0033	-825.8	3.3	14040	160
HC 813B	252137	leaf	Pit A		0.0970	0.0007	-903.0	0.7	18740	60
HC 817B	252138	leaf	Pit 3	C-4	0.0025	0.0006	-997.5	0.6	48200	2000
RLP 714B	216511	cup	Pit 91	GJM 372/L-9	0.0186	0.0005	-981.4	0.5	32000	240
HC 732B	218584	acorn frag	LACM 1814		0.0024	0.0005	-997.6	0.5	48500	1600
HC 573B	198383	leaf	Pit 91	RLP 1414A/N-7	0.0349	0.0009	-965.1	0.9	26950	210
RLP 690B	212957	leaf	Pit 91	GJM 841/L-5	0.0119	0.0009	-988.1	0.9	35600	640
Three-petal bedstraw (*Galium trifidum* L., Gentianales: Rubiaceae)										
HC 566B	198377	nutlets	Pit 3		0.0059	0.0047	-994.1	4.7	>33600	

Monterey cypress (*Hesperocyparis macrocarpa* (Hartw.) Bartel, Pinales: Cupressaceae)										
RLP 540B	193861	seed	Pit91	RLP 959/E-5	0.0008	0.0005	-999.2	0.5	>50800	
HC 131909B	252176	portion of cone	Pit 3	D-2	0.1577	0.0007	-842.3	0.7	14835	40
RLP 603B	218599	portion of cone	Pit 91	RLP 953/ E-4	0.0015	0.0004	-998.5	0.4	52100	2200
RLP 604B	218600	portion of cone	Pit 91	RLP 914/ F-7	0.0027	0.0005	-997.3	0.5	47500	1500
RLP 609B	218601	portion of cone	Pit 91	RLP 926/ F-3	0.0018	0.0004	-998.2	0.4	50900	1600
RLP 612B	218602	portion of cone	Pit 91	RLP 897/ G-4	0.0015	0.0003	-998.5	0.3	52400	1900
RLP 614B	218603	portion of cone	Pit 91	GJM 834/ F-6	0.0012	0.0003	-998.8	0.3	53900	2300
RLP 618B	218604	portion of cone	Pit 91	GJM 898/ F-5	0.0024	0.0005	-997.6	0.5	48500	1800
RLP 677B	218605	portion of cone	Pit 91	RLP 1228A/ F-6	0.0018	0.0003	-998.2	0.3	50600	1500
RLP 679B	218606	portion of cone	Pit 91	RLP 1248A/ E05	0.0014	0.0003	-998.6	0.3	52500	1900
RLP 535B	193856	seed	Pit91	GJM 651/F-5	0.0057	0.0013	-994.3	1.3	41600	1800
RLP 536B	193857	seed	Pit91	GJM 651/F-5	0.0035	0.0012	-996.5	1.2	45000	2800
RLP 541B	193862	seed	Pit91	RLP 923/E-7	0.0023	0.0006	-997.7	0.6	48700	2200
RLP 542B	193863	seed	Pit91	RLP 923/E-7	0.0007	0.0005	-999.3	0.5	>51200	

RLP 543B	193864	seed	Pit91	RLP 923/E-7	0.0008	0.0005	-999.2	0.5	>50800	
RLP 607B	212927	portion of cone	Pit 91	RLP 917/F-4	0.0007	0.0006	-999.3	0.6	>50300	
RLP 610B	212928	portion of cone	Pit 91	GJM 797/ F-4	0.0010	0.0006	-999.0	0.6	>48900	
RLP 613B	212929	portion of cone	Pit 91	GJM 834/ F-6	0.0013	0.0006	-998.7	0.6	53100	3700
RLP 616B	212930	portion of cone	Pit 91	GJM 844/F-5	0.0000	0.0006	-1000.0	0.6	>53500	
RLP 620B	212931	portion of cone	Pit 91	GJM 797/ F-4	0.0001	0.0006	-999.9	0.6	>53300	
RLP 622B	212932	portion of cone	Pit 91	RLP 929/E-6	0.0004	0.0006	-999.6	0.6	>51700	
RLP 623B	212933	portion of cone	Pit 91	GJM 834/F-6	0.0004	0.0006	-999.6	0.6	>51600	
RLP 625B	212934	portion of cone	Pit 91	RLP 917/F-4	0.0000	0.0006	-1000.0	0.6	>53500	
RLP 635B	212944	portion of cone	Pit 91	RLP 930/E-6	0.0007	0.0006	-999.3	0.6	>50100	
RLP 647B	212945	portion of cone	Pit 91	GJM 850/F-6	0.0008	0.0006	-999.2	0.6	>49900	
RLP 651B	212946	portion of cone	Pit 91	RLP 959/E-5	0.0004	0.0006	-999.6	0.6	>51600	

RLP 652B	212947	portion of cone	Pit 91	RLP 959/E-5	0.0014	0.0006	-998.6	0.6	52600	3500
RLP 653B	212948	portion of cone	Pit 91	RLP 959/E-5	0.0003	0.0006	-999.7	0.6	>52200	
RLP 654B	212949	portion of cone	Pit 91	RLP 959/E-5	0.0008	0.0006	-999.2	0.6	>49700	
California juniper (*Juniperus californica* Carrière, Pinales: Cupressaceae)										
HC 696B	216493	1 seed	Pit A		0.0617	0.0006	-938.3	0.6	22370	80
HC 697B	216494	1 seed	Pit 3		0.0020	0.0005	-998.0	0.5	50000	2100
HC 699B	216495	1 seed	Pit 3		0.0009	0.0005	-999.1	0.5	>50300	
HC 700B	216496	1 seed	Pit 3		0.0006	0.0005	-999.4	0.5	>49200	
HC 705B	216502	1 seed	Pit A		0.0009	0.0005	-999.1	0.5	>50300	
HC 706B	216503	1 seed	Pit A		0.0010	0.0005	-999.0	0.5	>44600	
HC 707B	216504	1 seed	Pit A		0.0625	0.0006	-937.5	0.6	22270	80
RLP 718B	216514	1 seed	Pit 91	GJM 288/M-9	0.0493	0.0006	-950.7	0.6	24180	100
HC 729B	218582	1 seed	Pit 4		0.0730	0.0004	-927.0	0.4	21025	50
HC 730B	218583	2 seed	Pit 5		0.0714	0.0004	-928.6	0.4	21200	60
HC 734B	218585	1 seed	LACM 1814		0.0002	0.0003	-999.8	0.3	>57300	
HC 574B	198384	1 seed	Pit 3		0.0008	0.0005	-999.2	0.5	>50800	
HC 577B	198387	1 seed	Pit A		0.0016	0.0005	-998.4	0.5	51800	2500

HC 686B	212954	1 seed	Pit A		0.0639	0.0006	-936.1	0.6	22090	80
HC 687B	212955	1 seed	Pit 3		0.0004	0.0006	-999.6	0.6	>51600	
HC 688B	212956	1 seed	Pit A		0.0002	0.0006	-999.8	0.6	>52700	
RLP 436B	252126	1 seed	Pit 91	GJM	0.0703	0.0006	-929.7	0.6	21330	80
RLP 1442B	252174	1 seed	Pit 3	D-2	0.0009	0.0005	-999.1	0.5	>50300	
RLP 1468B	252175	1 seed	Pit A		0.0009	0.0005	-999.1	0.5	>50300	
RLP 533B	193854	1 seed	Pit91	GJM 568/L-5	0.0046	0.0005	-995.4	0.5	43230	940
RLP 534B	193855	1 seed	Pit91	GJM 341/I-6	0.0452	0.0006	-954.8	0.6	24870	110
RLP 539B	193860	1 seed	Pit91	GJM 288/M-9	0.0710	0.0006	-929.0	0.6	21250	70
Rocky Mountain juniper (*Juniperus* cf. *scopulorum* Sarg., Pinales: Cupressaceae)										
HC 691B	216488	1 seed	Pit 13		0.0922	0.0006	-907.8	0.6	19150	60
HC 692B	216489	1 seed	Pit 13		0.0946	0.0006	-905.4	0.6	18940	60
HC 693B	216490	1 seed	Pit 60		0.0404	0.0006	-959.6	0.6	25770	120
HC 694B	216491	1 seed	Pit 60		0.0380	0.0006	-962.0	0.6	26270	130
HC 695B	216492	1 seed	Pit 4		0.0740	0.0006	-926.0	0.6	20920	70
HC 708B	216505	1 seed	Pit 67		0.0008	0.0005	-999.2	0.5	>50800	
HC 709B	216506	1 seed	Pit 67		0.0018	0.0005	-998.2	0.5	50700	2300
HC 710B	216507	1 seed	Pit A		0.0123	0.0051	-987.7	5.1	35300	3300
HC 711B	216508	1 seed	Pit A		0.0014	0.0005	-998.6	0.5	52500	2900
HC 712B	216509	1 seed	Pit 67		0.1805	0.0008	-819.5	0.8	13750	40

HC 713B	216510	1 seed	Pit 67		0.0022	0.0020	-997.8	2.0	>40800	
HC 745B	218589	1 seed	Pit 81		0.0154	0.0004	-984.6	0.4	33510	200
HC 746B	218590	1 seed	Pit 81		0.0156	0.0004	-984.4	0.4	33450	200
HC 748B	218596	2 seed	Pit 82		0.0221	0.0004	-977.9	0.4	30640	160
HC 749B	218597	2 seed	Pit 82		0.0279	0.0004	-972.1	0.4	28760	120
HC 750B	218598	2 seed	Pit 82		0.0270	0.0004	-973.0	0.4	29000	120
HC 575B	198385	1 seed	Pit 4		0.0316	0.0006	-968.4	0.6	27740	150
HC 576B	198386	1 seed	Pit 101		0.2040	0.0008	-796.0	0.8	12770	35
HC 674B	212951	1 seed	Pit 91	GJM 494/G-4	0.0147	0.0006	-985.3	0.6	33890	350
HC 684B	212952	1 seed	Pit 13		0.0011	0.0006	-998.9	0.6	>48500	
HC 685B	212953	1 seed	Pit 4		0.0263	0.0006	-973.7	0.6	29240	200
RLP 683B	252127	1 seed	Pit 91	GJM	0.0217	0.0006	-978.3	0.6	30770	220
HC 757B	252129	1 seed	Pit 91	GJM	0.0025	0.0006	-997.5	0.6	48300	2100
RLP 763B	252130	1 seed	Pit 91	GJM	0.1308	0.0008	-869.2	0.8	16335	50
RLP 782B	252131	1 seed	Pit 91	RLP	0.0013	0.0006	-998.7	0.6	53700	4000
RLP 1005B	252139	1 seed	Pit 91	GJM	0.0365	0.0006	-963.5	0.6	26600	140
RLP 1016B	252140	1 seed	Pit 91	GJM	0.1609	0.0007	-839.1	0.7	14675	40
RLP 1022B	252142	1 seed	Pit 91	GJM	0.0782	0.0006	-921.8	0.6	20470	70
RLP 1053B	252148	1 seed	Pit 91	GJM	0.0372	0.0006	-962.8	0.6	26430	130
RLP 1080B	252168	1 seed	Pit 91	RLP	0.0375	0.0005	-962.5	0.5	26370	120
RLP 1082B	252170	1 seed	Pit 91	RLP	0.1013	0.0008	-898.7	0.8	18390	70

RLP 1083B	252171	1 seed	Pit 91	RLP	0.0784	0.0007	-921.6	0.7	20450	80
RLP 553B	193873	1 seed	Pit 91	RLP 923/E-7	0.0156	0.0005	-984.4	0.5	33440	280
RLP 561B	193881	1 seed	Pit 67		0.0010	0.0005	-999.0	0.5	>49900	
Bishop pine (*Pinus muricata* D. Don, Pinales: Pinaceae)										
RLP 556B	193876	portion of cone	Pit 9		0.0008	0.0005	-999.2	0.5	>50800	
RLP 557B	193877	2 seeds	Pit 9		0.0003	0.0005	-999.7	0.5	>53400	
Monterey pine (*Pinus radiata* D. Don, Pinales: Pinaceae)										
RLP 552B	193872	portion of cone	Pit91	RLP 923/E-7	0.0018	0.0005	-998.2	0.5	50900	2400
Grey pine (*Pinus sabiniana* D. Don, Pinales: Pinaceae)										
RLP 682B	212950	portion of seed	Pit 91	RLP 1401 A/E-6	0.0000	0.0006	-1000.0	0.6	>53700	
Pine (*Pinus* sp., Pinales: Pinaceae)										
RLP 550B	193870	seed	Pit91	RLP 923/E-7	0.0005	0.0009	-999.5	0.9	>49100	
RLP 551B	193871	seed	Pit91	RLP 923/E-7	0.0021	0.0007	-997.9	0.7	49600	2800
RLP 552B	193872	portion of cone	Pit91	RLP 923/E-7	0.0018	0.0005	-998.2	0.5	50900	2400
RLP 558B	193878	portion of cone	Pit 9		0.0003	0.0005	-999.7	0.5	>53400	
RLP 559B	193879	portion of cone	Pit 9		-0.0002	-0.0005	-1000.2	-0.5	>55200	

RLP 549B	193869	1 seed	Pit91	RLP 923/E-7	0.0010	0.0006	-999.0	0.6	>51700	
RLP 626B	212935	char. Scale	Pit 91	GJM 651/F-5	0.0002	0.0006	-999.8	0.6	>52700	
RLP 627B	212936	char. Scale	Pit 91	GJM 651/F-5	-0.0002	-0.0006	-1000.2	-0.6	>53700	
RLP 628B	212937	char. Scale	Pit 91	GJM 651/F-5	-0.0001	-0.0006	-1000.1	-0.6	>53700	
RLP 629B	212938	char. Scale	Pit 91	GJM 651/F-5	-0.0003	-0.0006	-1000.3	-0.6	>53700	
RLP 630B	212939	char. Scale	Pit 91	GJM 651/F-5	-0.0002	-0.0006	-1000.2	-0.6	>53700	
RLP 631B	212940	char. Scale	Pit 91	GJM 651/F-5	0.0005	0.0006	-999.5	0.6	>51000	
RLP 632B	212941	char. Scale	Pit 91	GJM 651/F-5	0.0001	0.0006	-999.9	0.6	>53000	
RLP 633B	212942	char. Scale	Pit 91	GJM 651/F-5	0.0004	0.0006	-999.6	0.6	>51500	
RLP 634B	212943	char. Scale	Pit 91	GJM 651/F-5	0.0001	0.0006	-999.9	0.6	>53200	
Broadfruit bur reed (*Sparganium eurycarpum* Engelm. ex A. Gray, Poales: Typhaceae)										
RLP 728B	218581	2 seed	Pit 92	GJM 433/G-3	0.0032	0.0005	-996.8	0.5	46100	1200
Grass (Poales: Poaceae)										
RLP 1084B	252172	seed	Pit 91	GJM	0.3002	0.0010	-699.8	1.0	9665	30
Barley (*Hordeum* sp., Poales: Poaceae: Pooideae: Triticodae: Triticeae)										
RLP 1071B	252158	rachis and glumes and sterile floret	Pit 91	GJM	0.9477	0.0088	-52.3	8.8	430	80

California sycamore (*Platanus racemosa* Nutt., Proteales: Platanacea)										
RLP 1021B	252141	achene	Pit 91	GJM	1.4429	0.0037	442.9	3.7	MODERN	
RLP 1037B	252146	achene	Pit 91	GJM	1.4338	0.0030	433.8	3.0	MODERN	
RLP 1052B	252147	achene	Pit 91	GJM	1.4636	0.0030	463.6	3.0	MODERN	
RLP 1064B	252150	achene	Pit 91	GJM	1.4891	0.0040	489.1	4.0	MODERN	
RLP 1068B	252153	achene	Pit 91	GJM	1.4276	0.0032	427.6	3.2	MODERN	
RLP 1081B	252169	achene	Pit 91	RLP	1.3859	0.0029	385.9	2.9	MODERN	
RLP 722B	218577	1 achene	Pit 91	GJM 342/H-9	0.2452	0.0008	-754.8	0.8	11295	30
RLP 723B	218578	2 achenes	Pit 91	GJM 342/H-9	1.4376	0.0032	437.6	3.2	MODERN	
RLP 555B	193875	achene	Pit 91	GJM 342/H-9	1.2177	0.0020	217.7	2.0	MODERN	
RLP 765B	224292	achene	Pit 91	GJM 408/L-4	1.4141	0.0027	414.1	2.7	MODERN	
White water buttercup (*Ranunculus aquatilis* L., Ranunculales: Ranunculaceae)										
RLP 1066B	252151	achene	Pit 91	GJM	0.0089	0.0013	-991.1	1.3	37900	1200
Chamise (*Adenostoma fasciculatum* Hook. & Arn., Rosales: Rosaceae: Amygdaloideae: Sorbarieae)										
RLP 719B	216515	4 achenes	Pit 91	GJM 667/G-5	0.0016	0.0017	-998.4	1.7	>42600	
RLP 569B	198380	achene	Pit 91	GJM 667/G-5	0.0000	-0.0017	-1000.0	-1.7	>45700	
Boxelder maple (*Acer negundo* L., Sapindales: Sapindaceae)										
RLP 1024B	252145	pericarp	Pit 91	GJM	0.1950	0.0016	-805.0	1.6	13130	70
RLP 1085B	252173	pericarp	Pit 91	GJM	0.2078	0.0008	-792.2	0.8	12620	35
HC 702B	216486	pericarp	Pit 101		0.1941	0.0027	-805.9	2.7	13170	120

RLP 721B	216487	pericarp	Pit 91	GJM 338/H-8	1.4610	0.0038	461.0	3.8	Modern	
RLP 554B	193874	pericarp	Pit 91	GJM 338/H-8	1.4596	0.0029	459.6	2.9	Modern	
HC 701B	216497	pericarp	Pit 3		0.2018	0.0011	-798.2	1.1	12855	45
HC 562B	198373	pericarp	Pit 3		0.1932	0.0012	-806.8	1.2	13205	50
HC 563B	198374	pericarp	Pit 3		0.1868	0.0013	-813.2	1.3	13480	60
Parish's purple nightshade (*Solanum parishii* A. Heller, Solanales: Solanaceae)										
RLP 1063B	252149	seed	Pit 91	GJM	0.9624	0.0030	-37.6	3.0	305	30
RLP 1072B	252159	seed	Pit 91	GJM	0.5448	0.0037	-455.2	3.7	4880	60

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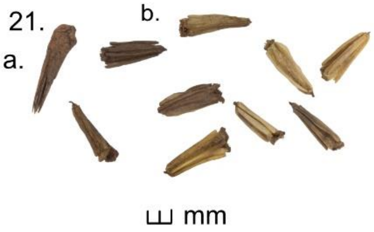

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Figure A-3: Select examples of identified plant fossils in order of appearance in AMS radiocarbon chronology 1) Pinus muricata cone (HC 1449B) 2) Pinus radiata cone scale (HC 552B) 3) Hesperocyparis macrocarpa 2 cones (a. RLP 604B b. RLP 677B) 4) Pinus sabiniana seed (RLP 682B) 5) Arctostaphylos glauca fused nutlets (RLP 544B) 6) Arctostaphylos sp. *fused nutlets (HC 735B) 7) Sparganyum eurycarpum seed (RLP 728B) 8) Cornus sericea seed (HC 703B) 9) Adenostonum fasciculatum 10 achenes (RLP 569B) 10) Balsamhoriza deltoidea 5 achenes (RLP 568B) 11) Ranuncululs aquatilis 7 achenes (RLP 1066B) 12) Galium trifidum 2 nutlets (HC 566B) 13) Oenanthe sarmentosa 5 fruit (RLP 571B) 14) Juniperus californica 1 seed (RLP 533B) 15) Juniperus* cf. *scopulorum 3 seeds (a. 2 seeds RLP 782B b. 1 seed RLP 763B) 16) Quercus agrifolia acorn (HC 796B) 17) Quercus* cf. *dumosa galls (RLP 717B) 18) Sambucus mexicana seed (RLP 720B) 19) Acer macrophyllum pericarp (RLP 1085B) 20) Atriplex* cf. *lentiformis* achene (RLP 1073B) *21) Platanus racemosa (a. 1 fossil achene RLP 722B b. 9 modern achenes RLP 1069) 22) Madia elegans 2 achenes (RLP 1074B) 23)* Poaceae seed (RLP 1048B) *24) Deinandra fasciculata 24 achenes (RLP 567B) 25) Hordeum* sp. *rachis and glumes* (RLP 1071B) *26) Solanum parishii 6 seeds (RLP 1063B)*

Table A-7: CRACLE Climate Estimates by Binned 2,000 Year Period

Time (ka)	**annual mean temp (bio1)**	**annual precipitation (bio12)**	**precipitation of coldest quarter (bio19)**
54	138.3827	615.1823	373.8319
52	138.3827	615.1823	373.8319
50	138.6745	625.5215	286.5298
48	137.2156	1101.125	530.5279
46	138.3827	620.3519	273.0987

44	136.3402	604.8431	282.0528
42	127.2948	604.8431	530.5279
40	138.9663	604.8431	188.0352
38	95.78153	604.8431	467.8495
36	143.0513	413.5679	532.7664
34	143.0513	413.5679	532.7664
32	142.7595	398.0591	170.1271
30	142.7595	398.0591	170.1271
28	151	374	174
27	151	374	174
26	142.4678	367.0415	167.8886
24	65.66906	426.0949	86.2704
22	142.7595	398.0591	170.1271
20	43.1352	424.4067	88.25149
18	142.7595	398.0591	170.1271
16	136.3402	682.3871	185.7967
14	145.3846	491.1119	268.6179
12	150.34	377.3807	264.1447
10	94.03079	780.6095	190.2737
8	*No data*	*No data*	*No data*
6	*No data*	*No data*	*No data*
4	*No data*	*No data*	*No data*
2	166.01	354.54	188.9438
0	147.72	578.9951	248.4751