Vegetation history along the eastern, desert escarpment of the Sierra San Pedro Mártir, Baja California, Mexico

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ABSTRACT

Plant macrofossils from 38 packrat middens spanning the last ~33,000 cal yr BP record vegetation between ~650 and 900 m elevation along the eastern escarpment of the Sierra San Pedro Mártir, northern Baja California. The middens span most of the Holocene, with a gap between ~4600 and 1800 cal yr BP, but coverage in the Pleistocene is uneven with a larger hiatus between 23,100 and 14,400 cal yr BP. The midden flora is relatively stable from the Pleistocene to Holocene. Exceptions include *Pinus californiarum*, *Juniperus californica* and other chaparral elements that were most abundant >23,100 cal yr BP and declined after 14,400 cal yr BP. Despite being near the chaparral/woodland-desertscrub ecotone during glacial times, the midden assemblages reflect none of the climatic reversals evident in the glacial or marine record, and this is corroborated by a nearby semi-continuous pollen stratigraphy from lake sediments. Regular appearance of C_4 grasses and summer-flowering annuals since 13,600 cal yr BP indicates occurrence of summer rainfall equivalent to modern (JAS average of ~80–90 mm). This casts doubt on the claim, based on temperature proxies from marine sediments in the Guaymas Basin, that monsoonal development in the northern Gulf and Arizona was delayed until after 6200 cal yr BP.

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Introduction

The Baja California peninsula is rich in both biodiversity and endemism, but it is also increasingly threatened by development and cross-border tourism. The peninsula's touristic potential is enhanced by its scenic coastlines juxtaposing desert and sea, low-cost coastal real estate, proximity to large population centers in adjacent California, and ease of travel from California, Nevada, and Arizona. Of concern, however, is the scale and speed of recent development, mostly in the form of direct joint ventures between Mexican and foreign partners, which puts into peril the same ecological setting that makes Baja California a popular destination. Adding to the challenge are projected climatic changes and non-native plant invasions that could possibly trigger a spatial reorganization of ecosystems. For example, faunal range shifts in Mexico projected by 2055 include high species turnover rates (>40% of species) and colonization of 50 to 100 new animal species in the Sierra Juárez and San Pedro Martír (Peterson et al., 2002). The range of many endemic plants is also projected to change in the region (Loarie et al., 2008). As a result, land managers will be faced with ongoing plant and animal migrations and the need to effectively manage complex and ever-changing resources. Historical information about ecosystem resilience to past climatic changes can provide useful insights, but there has been very little paleoecological work in the peninsula compared to the adjacent southwestern U.S., which has a long history of packrat midden research. The only midden studies in Baja California are in the Central Desert area near San Fernando and Cataviña (Peñalba and Van Devender, 1997; Peñalba and Van Devender, 1998) and a single midden from Sierra San Francisco (Rhode, 2002) (Fig. 1).

Here we use 38 packrat middens to reconstruct vegetation at the base of the eastern escarpment of the peninsula's highest mountain, the Sierra San Pedro Martir, 200 km south of USA–Mexico border. This study is part of a ~500-km north–south transect of midden series in granite substrates from Joshua Tree National Park in southeastern California (Holmgren et al., 2010) to Cataviña in central Baja California designed to evaluate plant community assembly in the western Sonoran Desert on millennial timescales. Because desert refugia have yet to be identified, for example, we can only speculate about the glacial distribution of many Sonoran Desert plants and their migrational pathways during the Holocene. This prevents us from using patterns of past vegetation change and stability to help anticipate vegetation sensitivity and resistance to global change, and to inform conservation and restoration initiatives.

Study area

Physiographic setting

Baja California is traversed by the Peninsular Ranges, a north–south trending backbone of westward-tilted granitic fault block
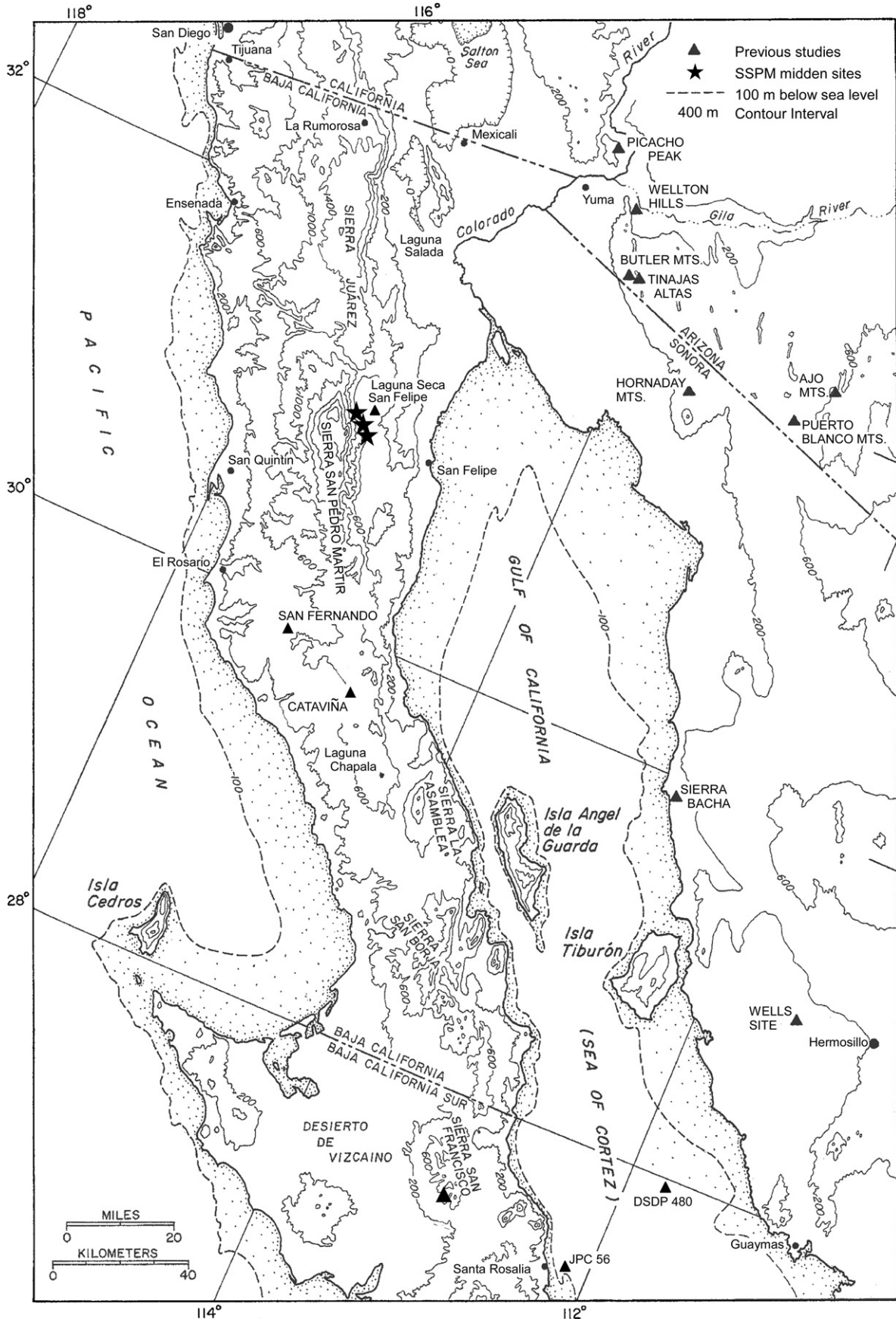

Figure 1. Topographic map of the study area showing the location of previous midden studies along with the SSPM midden sites. Land areas that would have been exposed during the last glacial period are indicated by the 100 m below sea level contour line and stippled pattern.

ranges that stretches from southern California into Baja California and includes the Sierra Juárez and Sierra San Pedro Mártir (SSPM). The highest peaks within the Peninsular Ranges are found within the SSPM, including Picacho del Diablo at 3095 m. To the west, the SSPM slopes gently towards the Pacific coast, whereas to the east it is bounded by a steep escarpment that abruptly drops down ~2500 m into the Santa Clara, San Felipe, and Chico Valleys, ~500 m above sea level. The port of San Felipe and the Gulf of California are only 30–50 km east of the SSPM escarpment.

It is along the base of this rugged eastern escarpment that we collected middens for this study (Fig. 1). Rock types exposed within the study area include Paleozoic metamorphic and plutonic rocks and Mesozoic batholitic rocks (Gastil et al., 1973; Gastil et al., 1975). The latter are predominantly granodiorites and tonalites that were most likely emplaced during Cretaceous magmatic arc activity and subsequently uplifted and tilted during the Pliocene–Quaternary following development of the San Andreas-Gulf of California transform system (Gastil et al., 1975; Silver and Chappell, 1988; O'Connor and Chase, 1989). Quaternary alluvial sediments blanket the valleys to the east at the foot of the range (Walker and Thompson, 1968; Gastil et al., 1975).

Climate

The climate of Baja California, and precipitation in particular, varies greatly due to the peninsula's latitudinal range, complex topography, and location between water bodies with vastly different sea surface temperatures. Although most of the Baja California peninsula is extremely arid due to the nearly year-round influence of the North Pacific High, precipitation patterns vary sub-regionally and seasonally (Fig. 2) as a result of modulation by the mid-latitude westerlies in the winter and by the North American Monsoon system in the summer. During winter, the North Pacific High weakens and migrates to the southeast, while expansion of the Aleutian Low shifts the Pacific storm track southward and brings precipitation derived from mid-latitude cyclones embedded within the westerlies into northern Baja California (Hastings and Turner, 1965; Markham, 1972; Woodhouse, 1997). Winter precipitation peaks in January and is greatest in northern Baja California along the Pacific coast and western slopes of the Sierra Juárez and SSPM; the combination of wet winters and dry summers here represents a southern extension of the classic Mediterranean climate found to the north in California. Winter precipitation decreases both to the south away from the influence of the westerlies, and to the east as moisture is blocked by the Sierra Juárez and SSPM. These mountain ranges represent a nearly continuous barrier that produces a moderate rainshadow effect and notably asymmetrical precipitation receipts between the eastern and western-facing slopes. For example, the northern Gulf of California and San Felipe Desert receive only about one-fourth as much precipitation as the Mediterranean region on the Pacific coast at the same latitude (Hastings and Turner, 1965), making it Baja California's driest area. The Sierra Juárez and SSPM likewise block cool air from the Pacific, contributing to the extremely high temperatures found here (Markham, 1972).
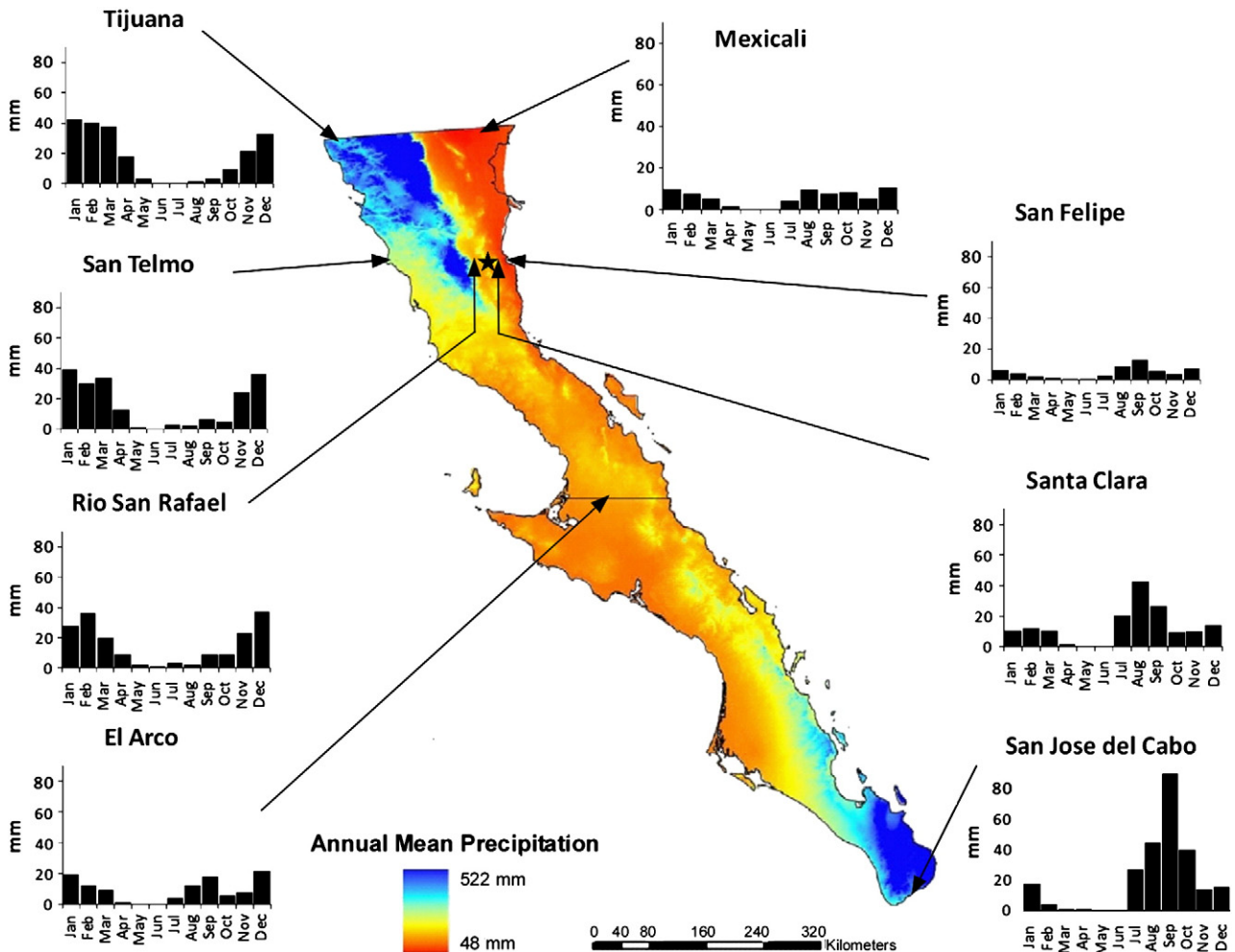

Figure 2. Precipitation patterns for Baja California. Modified from González-Abraham et al., 2008. Inset precipitation graphs constructed from World Meteorological Organization CLICOM data at the Servicio Meteorológico Nacional-Mexico.

Summer precipitation, on the other hand, is the result of convective activity associated with the North American monsoon (Carleton, 1987; Cavazos and Hastenrath, 1990; Burnett, 1994; Adams and Comrie, 1997; Comrie and Glenn, 1998). The core region of the North American monsoon is centered over the Sierra Madre Occidental on the Mexican mainland, with a steep decline in precipitation westward towards the Gulf of California and the Baja California peninsula (Hastings and Turner, 1965; Adams and Comrie, 1997). Summer precipitation totals are therefore greatest along the southeastern tip of the peninsula, which is located furthest east. This area is characterized by a late summer rainfall maximum and very low winter precipitation. Additional late summer–early fall precipitation is derived from recurving tropical storms, or "chubascos," which can impact the entire peninsula (Hastings and Turner, 1965; Markham, 1972), especially during September and October as low pressure troughs and cut off lows steer storms into the region (Smith, 1986; Webb and Betancourt, 1992). This tropical storm activity is most likely the reason that summer precipitation in southern Baja California peaks in September rather than July and August, as is typical in other North American monsoon regions (Adams and Comrie, 1997; Stensrud et al., 1997). Central Baja California, located between the key winter and summer precipitation regimes, exhibits bimodal precipitation seasonality.

Our study area in northeastern Baja California is extremely hot and arid due to the extensive lowlands, influence of the Pacific High, the rainshadow created by the SSPM, and its location at the extreme western limit of the North America monsoon. The longest climate record (1948–2008) for our study area comes from San Felipe, located on the coast ~45 km east of the midden sites at 10 m elevation (Fig. 1). The average annual temperature at San Felipe is 19°C, with a range from 10.9°C in January to 30.1°C in July, and the average annual precipitation is 56 mm, with marginally more precipitation falling in summer (JAS) than in winter (DJF). The average annual precipitation at the midden sites (647–899 m) is certainly greater than on the coast because precipitation increases with elevation in the SSPM. Although the records are shorter, data from two additional stations can help constrain precipitation at the midden sites. The Santa Clara station (1962–2008), located at 410 m elevation and within 19 km of the midden sites, receives an annual average of 160 mm of precipitation, with 56% of it falling in summer (Fig. 2). The Rio San Rafael station (1958–1974), located at 1700 m elevation and within 36 km of the midden sites, recorded an annual average of 179 mm of precipitation, with 57% of it falling in winter. Based on these stations, we can estimate that average annual precipitation at the middens sites is roughly between 160 and 180 mm and is most likely derived approximately equally from summer and winter precipitation sources.

Vegetation

Vegetation along the eastern flank of the SSPM is characterized by the transition from the Lower Colorado Valley subdivision of the Sonoran Desert (also known as Colorado Desert) in the foothills to California Chaparral, which then grades into Sierran Montane Conifer Forest with pockets of Great Basin Conifer Woodland as elevation increases (Turner and Brown, 1982). Vegetation at the midden sites, located at the base of the SSPM between 647 and 899 m, includes both Sonoran Desert and California chaparral elements. A listing of all plant taxa and common names is available in Table 1. Vegetation here is dominated by *Ambrosia dumosa*, *Bursera hindsiana*, *Bursera microphylla*, *Cercidium microphyllum*, *Croton*, *Eriogonum wrightii*, *Erythrina flabelliformis*, *Euphorbia tomentulosa*, *Fouquieria splendens*, *Hyptis emoryi*, *Justicia californica*, *Nolina*, *Olneya tesota*, *Pleurocoronis pluriseta*, and *Viguiera parishii*. Also present are scattered individuals of *Abutilon palmeri*, *Acacia greggii*, *Prosopis glandulosa* var. *torreyana*, *Quercus turbinella*, *Q. chrysolepis*; shrubs and herbs including *Acalypha*

californica, *Brickellia* spp., *Cheilanthes*, *Cryptantha*, *Encelia farinosa*, *Eriogonum fasciculatum*, *Euphorbia misera*, *Janusia gracilis*, *Lotus* cf. *scoparius*, *Lycium berlandieri*, *Gutierrezia*, *Machaeranthera pinnatifida*, *Notholaena*, *Penstemon*, *Physalis*, *Rhus*, *Solanum*, *Tragia urticifolia*, and *Trixis californica*; cacti and succulents including *Agave* cf. *cerulata*, *Agave deserti*, *Echinocereus* spp., *Ferocactus*, *Lophocereus schottii*, *Mammillaria*, *Opuntia acanthocarpa*, *Opuntia ramosissima*, *Opuntia tesajo*, *Pachycereus pringlei*, and *Yucca*; and grasses such as *Bouteloua curtipendula*, *Heteropogon contortus*, and *Stipa*. The more mesic species *Juniperus californica* was found only at one north-facing site (Driftwood Canyon #630, elevation 790 m), whereas *Larrea tridentata*, the dominant species in the valleys, was found only at one of the lowest sites with a south-facing slope (Waterfall Canyon #952, elevation 694 m, undated midden).

Methods

Midden collection and processing

We collected 76 middens between 647 and 899 m along the eastern flank of the SSPM over the course of two field seasons, with 44 middens collected during the spring of 2001 and 32 middens collected during the spring of 2002. A minimum of 500 g was collected from each midden, wherever possible leaving enough material *in situ* to allow for future resampling. The outer midden surface, which can contain modern contaminants, was removed in the field using a rock hammer and chisel. Likewise, middens containing layers were split along the bedding planes and the resulting chunks were processed and analyzed separately. Plants within 100 m of the site were identified and their relative abundances quantified.

In the laboratory, middens were processed according to well-established procedures (Spaulding et al., 1990). Middens were inspected and any remaining surface material was removed. Middens were then weighed, soaked in water for several days to weeks until completely disaggregated, wet screened, and dried in a low temperature oven. Finally, plant macrofossils (e.g., twigs, leaves, seeds, flowers, and fruits) were sorted and identified using a binocular stereomicroscope (0.75×–11.25×) and quantified on a relative abundance scale of 1 to 5 where $0 = 0$ fragments, $1 = 1$ fragment, $2 = 2–25$, $2.5 = 26–50$, $3 = 51–75$, $3.5 = 76–100$, $4 = 101–150$, $4.5 = 151–200$, and $5 \geq 200$ fragments.

Thirty eight middens were selected for radiocarbon dating based on midden condition and composition. Plant macrofossil materials for radiocarbon dating were pretreated and graphite targets prepared at the University of Arizona Desert Laboratory in Tucson, Arizona and measured by a tandem accelerator mass spectrometer (TAMS) at the University of Arizona-National Science Foundation Accelerator Facility. The Calib 5.0.2 Intcal04 calibration curve (Stuiver and Reimer, 1993) was used for samples <21,000 ^{14}C yr BP and the CalPal-2007-Hulu curve was used for samples >21,000 ^{14}C yr BP (www.calpal.de). Dates are plotted and reported herein as the midpoint of calibrated 2-sigma age ranges (Table 2).

Macrofossil identification

All pinyon pine needles found in the SSPM middens were single-needled pinyons. Traditionally, the single-needled pinyon pines growing along the eastern slope of the SSPM at lower elevations have been referred to as *Pinus monophylla*. More recent work, however, has resulted in the description of two additional one-needled varieties, *Pinus edulis* var. *fallax* and *Pinus californiarum*, based on needle diameter, the number of resin canals, and the number of stomatal rows (Bailey, 1987; Cole et al., 2008). The other pinyon species growing in the SSPM is *Pinus quadrifolia*, which generally has four needles per fascicle, but may have between three and five needles (Baldwin et al., 2002). This species is most commonly found in more

Table 1
Scientific and common names of plant taxa mentioned in the text.

Scientific name	Common name
Pteridophyta	
Polypodiaceae	
Cheilanthes sp.	Lipfren
Notholaena sp.	Cloak fern
Gymnospermae	
Cupressaceae	
Juniperus californica	California juniper
Pinaceae	
Pinus californiarum	California singleleaf pinyon
Pinus edulis	Colorado pinyon
Pinus edulis var. *fallax*	Arizona singleleaf pinyon
Pinus juarezensis	Sierra Juárez pinyon
Pinus monophylla	Singleleaf pinyon
Pinus quadrifolia	Parry pinyon pine
Angiospermae—Dicots	
Acanthaceae	
Justicia californica	Chuparosa
Amaranthaceae	
Iresine sp.	Bloodleaf
Anacardiaceae	
Rhus	Skunkbrush
Asteraceae	
Ambrosia cf. *carduacea*	Baja California ragweed
Ambrosia dumosa	Burro-weed
Brickellia cf. *atractyloides*	Spearleaf brickellbush
Brickellia cf. *californica*	California brickellbush
Encelia farinosa	Brittlebush
Ericameria	Goldenbush
Gutierrezia sp.	Snakeweed
Machaeranthera pinnatifida	Lacy tansyaster
Pleurocoronis pluriseta	Bush arrowleaf
Trixis californica	California trixis
Verbesina sp.	Crownbeard
Viguiera cf. *parishii*	Parish's golden eye
Boraginaceae	
Cryptantha	Cryptantha
Cryptantha pterocarya	Wingnut cryptantha
Brassicaceae	
Dithyrea wislizeni/californica	Tourist plant/shieldpod
Burseraceae	
Bursera microphylla	Torote
Bursera hindsiana	Copal
Cactaceae	
Echinocereus sp.	Hedgehog cactus
Cylindropuntia	Cholla
Ferocactus sp.	Barrel cactus
Lophocereus schottii	Senita cactus
Mammillaria sp.	Nipple cactus
Opuntia acanthocarpa	Buckhorn cholla
Opuntia ramosissima	Diamond cholla
Opuntia tesajo	Pencil cholla
Pachycereus pringlei	Cardón
Platyopuntia	Prickly pear
Ericaceae	
Arctostaphylos sp.	Manzanita
Euphorbiaceae	
Acalypha californica	California copperleaf
Croton	Croton
Ditaxis lanceolata	Narrowleaf silverbush
Euphorbia misera	Cliff spurge
Euphorbia tomentulosa	
Tragia urticifolia	Nettleleaf noseburn
Fabaceae	
Acacia greggii	Catclaw acacia
Cercidium microphyllum	Smallleaf palo verde
Erythrina flabelliformis	Coralbean
Lotus cf. *scoparius*	California broom
Olneya tesota	Ironwood
Prosopis glandulosa var. *torreyana*	Western honey mesquite
Fagaceae	
Quercus berberidifolia	Inland scrub oak
Quercus chrysolepis	Canyon live oak
Quercus cornelius-mulleri	Muller's oak
Quercus dumosa coastal	Sage scrub oak

Table 1 (*continued*)

Scientific name	Common name
Fagaceae	
Quercus john-tuckeri	Tucker's oak
Quercus durata	Leather oak
Quercus pacifica	Channel Island scrub oak
Quercus turbinella	Shrub live oak
Fouquieriaceae	
Fouquieria splendens	Ocotillo
Hydrophyllaceae	
Phacelia sp.	Scorpionweed
Lamiaceae	
Hyptis emoryi	Desert lavender
Salvia sp.	Sage
Loranthaceae	
Phoradendron californicum	Mesquite mistletoe
Malvaceae	
Abutilon palmeri	Palmer's Indian mallow
Malpighiaceae	
Janusia gracilis	Slender janusia
Nyctaginaceae	
Boerhavia sp.	Spiderling
Polygonaceae	
Eriogonum fasciculatum	California buckwheat
Eriogonum wrightii	Bastardsage
Rosaceae	
Cercocarpus betuloides	Mountain mahogany
Purshia tridentata	Antelope bitterbrush
Prunus sp.	
Rutaceae	
Thamnosma montana	Turpentine broom
Scrophulariaceae	
Castilleja	Indian paintbrush
Galvezia juncea	Baja bush snapdragon
Penstemon sp.	Beardtongue
Simmondsiaceae	
Simmondsia chinensis	Jojoba
Solanaceae	
Lycium berlandieri	Berlandier's wolfberry
Physalis sp.	Groundcherry
Solanum sp.	Nightshade
Zygophyllaceae	
Kallstroemia californica	California caltrop
Larrea tridentata	Creosote bush
Viscainoa geniculata	Guayacan
Angiospermae—Monocots	
Agavaceae	
Agave deserti	Desert agave
Agave cf. *cerulata*	n/a
Agave sp.	Agave
Nolina bigelovii	Bigelow's nolina
Yucca brevifolia	Joshua tree
Yucca sp.	Yucca
Poaceae	
Bothriochloa barbinodis	Cane bluestem
Bouteloua curtipendula	Side-oats grama
Digitaria californica	Arizona cottontop
Enneapogon sp.	Pappusgrass
Heteropogon contortus	Tanglehead
Panicum sp.	Panicgrass
Setaria sp.	Bristlegrass

mesic sites on the western flank of the SSPM between 1400 and 1900 m (Delgadillo Rodriguez, 2004). *P. quadrifolia* frequently hybridizes with *P. californiarum*, producing trees with an intermediate number of needles. Some botanists regard pinyons with five needles as a distinct species, *Pinus juarezensis*, and *P. quadrifolia* as a hybrid between it and *P. californiarum*, but others regard these species as synonymous (Lanner, 1974; Perry, 1991; Farjon and Styles, 1997; Lanner and Van Devender, 1998). Using the criteria described above, we identified the pinyon species growing along the flank of the SSPM today, as well as all the fossil material from within the middens, as *P. californiarum*. Similarly, a suite of eleven different characters

Table 2
Radiocarbon dates and site locations of rodent middens.

Midden designation	Latitude (°N)	Longitude (°W)	Elevation (m)	Aspect	¹⁴C Age	SD	Lab code	2σ calibrated age range (cal yr BP)	Calibrated age midpoint (cal yr BP)	Material dated
Driftwood Canyon 648A	30°56.20′	115°15.53′	692	N	583	30	AA51861	534–650	590	Prunus seed
Canada de los Burros 621	31°08.54′	115°25.57′	709	ENE	1450	34	AA54747	1298–1394	1345	Prunus seed
Canada de los Burros 614B	31°08.54′	115°25.65′	729	WNW	1539	39	AA51845	1350–1523	1435	Acorn
Canada el Diablito 626	31°03.50′	115°21.39′	893	S	1644	37	AA51848	1416–1686	1550	Quercus leaves
Canada de los Burros 614A	31°08.54′	115°25.65′	729	WNW	1808	35	AA51846	1621–1857	1740	Acorn
Canada de los Burros 624	31°08.43′	115°25.60′	733	ENE	4030	52	AA54741	4411–4807	4610	Quercus leaves
Canada el Diablito 625	31°03.53′	115°21.40′	893	N	4282	42	AA51849	4709–4968	4840	Quercus leaves
Driftwood Canyon 943	30°56.49′	115°15.45′	689	SSE	4320	51	AA51864	4827–5039	4930	Fabaceae leaves
Driftwood Canyon 631	30°56.37′	115°15.60′	647	N	4909	41	AA51863	5589–5721	5655	Quercus leaves
Canada de los Burros 622	31°08.56′	115°25.73′	740	WNW	4942	42	AA54742	5593–5840	5715	Quercus leaves
Canada de los Burros 623B	31°08.53′	115°25.70′	754	ESE	5290	45	AA51844	5938–6189	6065	Acorn
Canada de los Burros 623A	31°08.53′	115°25.70′	754	ESE	5314	42	AA54748	5950–6261	6105	Quercus leaves
Canada el Diablito 601	31°03.53′	115°21.44′	899	ENE	5390	61	AA51847	6001–6291	6145	Acorns
Canada de los Burros 642	31°08.44′	115°25.62′	718	NE	5627	46	AA51846	6308–6492	6400	Acorn
Driftwood Canyon 644C	30°56.23′	115°15.28′	692	NW	5649	45	AA51851	6311–6532	6420	Quercus leaves
Canada de los Burros 610	31°08.54′	115°25.69′	707	ESE	6577	46	AA54744	7425–7566	7495	Acorn
Driftwood Canyon 646B	30°56.27′	115°15.30′	673	NNW	6852	43	AA51865	7609–7787	7700	Quercus leaves
Driftwood Canyon 630	30°56.19′	115°15.33′	790	ENE	7480	56	AA51862	8186–8385	8285	Prosopis leaf
Waterfall Canyon 970A	30°56.06′	115°15.18′	650	NNE	7870	53	AA51841	8548–8976	8760	Acorns
Driftwood Canyon 628	30°56.27′	115°15.25′	722	ENE	7970	52	AA51844	8648–8997	8825	Acorns
Driftwood Canyon 644A	30°56.23′	115°15.28′	692	NW	8050	53	AA51853	8724–9120	8920	Acorns
Canada de los Burros 609	31°08.67′	115°25.67′	666	NW	8700	68	AA54743	9537–9907	9720	Prunus seed
Driftwood Canyon 629B	30°56.27′	115°15.32′	680	ENE	8890	59	AA51850	9767–10195	9980	Acorns
Driftwood Canyon 629A	30°56.27′	115°15.32′	680	ENE	8960	55	AA51852	9913–10229	10,070	Acorns
Driftwood Canyon 646C	30°56.27′	115°15.30′	673	NNW	9210	68	AA51859	10,553	10,395	Quercus leaves
Waterfall Divide 951A	30°56.12′	115°15.13′	648	NE	9730	60	AA51857	11,249	11,025	Quercus leaves
Waterfall Divide 951C	30°56.12′	115°15.13′	648	NE	9860	60	AA51840	11,598	11,390	Acorns
Canada el Diablito 643B	31°03.50′	115°21.41′	870	SSE	9880	60	AA51860	11,601	11,400	Quercus leaves
Driftwood Canyon 971	30°56.60′	115°15.64′	745	SSE	10,100	57	AA54734	11,976	11,690	Acorns
Driftwood Canyon 950	30°56.35′	115°15.61′	758	S	10,210	58	AA54738	12,138	11,895	Acorns
Driftwood Canyon 959B	30°56.51′	115°15.74′	~700	S	11,650	78	AA51842	13,691	13,505	Pinus cone scale
Waterfall Canyon 963	30°56.57′	115°15.16′	705	N	11,740	67	AA54735	13,748	13,585	Acorns
Driftwood Canyon 972A	30°56.60′	115°15.64′	745	SSE	12,330	70	AA54737	14,714	14,365	Acorns
Driftwood Canyon 985	30°56.51′	115°15.50′	720	SSE	19,410	120	AA54736	23,565	23,100	Acorns
Canada de los Burros 611	31°08.54′	115°25.69′	690	NNW	21,660	220	AA54745	26,690	25,935	Acorn
Driftwood Canyon 945B	30°56.49′	115°15.45′	689	SSE	22,750	180	AA51858	28,010	27,425	Juniperus stem
Driftwood Canyon 946	30°56.49′	115°15.45′	689	SSE	26,180	310	AA51843	31,224	30,795	Acorns
Driftwood Canyon 945C	30°56.49′	115°15.45′	689	SSE	28,590	340	AA54739	34,419	33,135	Juniperus stem

(Holmgren et al., 2010) was used to confirm that the juniper fossils found within the middens are *Juniperus californica*.

Identification of the scrub white oaks found within the middens was more problematic. Because highly convergent leaf form and frequent hybridization among the species have hampered taxonomic efforts, most scrub white oaks were formerly lumped together as *Quercus dumosa* (Nixon, 2002). Recent refinements in identification based on a suite of features including acorn size, shape, color, and stalk length, leaf margin spine tooth regularity, and trichome characteristics, in addition to leaf form, resulted in the splitting of *Quercus dumosa* (*sensu lato*) into *Q. dumosa sensu stricto*, *Q. berberidifolia*, *Q. cornelius-mulleri*, *Q. pacifica*, and *Q. durata* (Nixon and Steele, 1981; Nixon and Muller, 1994; Nixon, 2002). Of these, *Q. dumosa sensu stricto*, *Q. berberidifolia* and *Q. cornelius-mulleri* are found in northern Baja California.

Further complicating the matter, the name *Q. turbinella* was previously applied to scrub white oak populations found from Arizona into Texas and northern mainland Mexico (now the typical *Q. turbinella*), as well as to scrub white oaks in southern California and Baja California. The latter of these have since been reassigned to *Q. john-tuckeri* and *Q. cornelius-mulleri* (Nixon, 2002), but a few disjunct populations of the typical *Q. turbinella* are also found along the eastern slopes of the Sierra Juárez and Sierra San Pedro Mártir in Baja California, west of the main populations and overlapping with *Q. john-tuckeri* and *Q. cornelius-mulleri*.

Based on the characteristics outlined in Nixon (2002) and Hickman (1993), we identified *Q. turbinella* as the modern white scrub oak commonly growing at our field sites. In addition, the golden oak *Q. chrysolepis* was found growing in the study area at 850 m in Cañada el Diablito. Identifying fossil white scrub oaks from the midden material, however, presented a greater challenge than identifying living oaks. Our material did not match *Q. berberidifolia*, *Q. cornelius-mulleri*, or *Q. dumosa sensu stricto*, but demonstrated similarities to both *Q. john-tuckeri* and *Q. turbinella*. For example, the size of most fossil material was more similar to *Q. turbinella*, yet the fossil leaves lacked the presence of glandular trichomes interspersed among stellate trichomes that is characteristic of this species. Trichomes on fossil leaves were frequently eroded, however, so it is possible that the lack of glandular trichomes is due to poor preservation, rather than a true lack of this feature. Likewise, complete acorns, another often diagnostic feature, were uncommon in the middens. In the end, we were unable to distinguish between the two species and refer to our fossil material as *Q. cf.turbinella/john-tuckeri*.

Results

Radiocarbon dating

Radiocarbon dates for the SSPM middens range from 33,045 to 590 cal yr BP (Table 2). Fifteen middens date from the Pleistocene, including five middens from the full glacial period, three from the Bølling/Allerød, and seven from the latest Pleistocene. Twenty-three additional midden dates span the Holocene, with only two temporal gaps greater than 1000 yr. Six of these middens date from the early Holocene (10–8 ka), twelve date from the middle Holocene (8 ka),

and five date from the late Holocene (4 ka to present). In the Holocene, the most conspicuous gap in the midden record occurs from 4.6 to 1.8 ka. Elsewhere in the Southwest, gaps tend to occur in the middle Holocene (8 ka) (Webb and Betancourt, 1990).

Plant macrofossil assemblages

We identified a total of 81 taxa from the packrat midden macrofossils. Relative abundances of selected plant macrofossils

(after Spaulding et al., 1990) are summarized in Figure 3 and the complete dataset can be accessed online at http://esp.cr.usgs.gov/data/midden. Several patterns characterize the vegetation record from the SSPM. One notable trend was the glacial dominance of the California chaparral species *Q. turbinella/john-tuckeri*, *Juniperus californica*, and *P. californiarum*. Other California chaparral species present during the glacial include *Arctostaphylos*, *Cercocarpus betuloides*, and *Purshia tridentata*. With the exception of *Q. turbinella/john-tuckeri* and a single individual of *Juniperus californica*,

Figure 3. Plant macrofossil abundance through time for selected species.

these represent extra-local species that are no longer found at the study sites today.

During the latest Pleistocene–early Holocene, most of the California chaparral species disappeared from or became rare in the record and were replaced by Sonoran Desert elements including trees/large shrubs such as *A. greggii*, *Bursera* spp., *H. emoryi*, *Simmondsia chinensis* and *Viscainoa geniculata*; smaller shrubs and herbs such as *A. palmeri*, *Brickellia*, *Eriogonum* cf. *wrightii*, *Iresine* sp., *Kallstroemia californica*, and *Verbesina*, the cactus *Echinocereus*, and the grasses *Bothriochloa barbinodis*, *Bouteloua barbata*, *B. curtipendula*, *Enneapogon*, and *Panicum*. Whereas most Sonoran Desertscrub species appeared during or shortly after the glacial–interglacial transition, a few did not arrive until the middle- to late-Holocene. These species include *Ambrosia* cf. *carduacea/dumosa*, *F. splendens*, *Mammillaria*, *Dithyrea wislizeni/californica*, *P. pringlei*, and *T. urticifolia*.

Despite these changes, another notable trend was the persistence of many species throughout the entire period of record. A third of all species identified in the SSPM middens were found in the oldest middens (those dating to 23,100 cal yr BP or earlier), and were still present in the late Holocene. These persistent plants included several of the more common and abundant species found in the middens such as *Q. turbinella/john-tuckeri*, *Agave* spp., *Cylindropuntia*, *Digitaria californica*, *Encelia* cf. *farinosa*, *Ericameria*, *Ferocactus*, *Nolina* cf. *bigelovii*, *Physalis*, *Platyopuntia*, *P. glandulosa* var. *torreyana*, *Prunus*, *Rhus*, and *Viguiera deltoides*.

Discussion

Glacial-age middens from the SSPM are characterized by abundant *P. californiarum*, *Juniperus californica*, *Q. turbinella/john-tuckeri*, and other chaparral species that indicate that California chaparral extended downslope to at least 650 m. Although the SSPM record has a large gap from 23,100 to 14,400 cal yr BP, we note that both the pinyon and juniper macrofossil abundances are greater from 33,000 to 23,100 cal yr BP than after 14,400 cal yr BP. We generally avoid relying on variations in plant macrofossil abundances for key inferences, but we attribute this conspicuous and replicated difference to greater effective moisture prior to 23,100 cal yr BP than after 14,400 cal yr BP. There is corroborating evidence for this in the sediment and pollen stratigraphy of a 9.5-m core extracted from ~400 m elevation in Laguna Seca de San Felipe (LSSF), a dry playa ~17 km long N–S and 4 km wide E–W just 10–20 km east of the midden sites (Fig. 1) (Ortega-Guerrero et al., 1999; Lozano-García et al., 2002).

The LSSF core was sampled and analyzed for mean particle size, loss-on-ignition (LOI), magnetic susceptibility, and pollen. Age determinations were based on linear interpolation or extrapolation with depth of the six AMS ^{14}C dates of organic matter in bulk sediment (Ortega-Guerrero et al., 1999). The six dates were originally reported as ^{14}C yr BP have been calibrated to cal yr BP for our discussion. The core spans the last 70 ka with the last 4000 yr missing due to erosion. The core is characterized by dry conditions and eolian sedimentation before 45,000 cal yr BP, lake development from 45,000 to 14,000 cal yr BP with highest lake productivity between 40,000 and 30,000 cal yr BP, continued moist conditions from 14,000 to 7800 cal yr BP except for a drying episode ~13,000 cal yr BP, and desiccation ~7800 cal yr BP.

Pollen analyses were limited to the part of the core with adequate pollen preservation between 47,000 and 16,000 cal yr BP. Lozano-García et al. (2002) discriminate the LSSF core into four pollen zones. Zone 4 (47,000–44,000 cal yr BP) and Zone 3 (44,000–39,000 cal yr BP) are dominated by *Pinus*, *Juniperus*, and *Artemisia* pollen. Zone 2 (39,000–26,000 cal yr BP) registers an increase in *Juniperus* and aquatic taxa and a decrease in *Pinus*. Zone 1 (26,000–16,000 cal yr BP) has the highest percentages of *Juniperus* with moderate percentages of *Pinus*. The higher *Juniperus* percentages in Zones 2 and 1 are seen as maximum lowering of woodland elements from the east slope of the Sierra San Pedro Martir to the edge of the San Felipe Basin ~500 m elevation. Both the sediment

and pollen stratigraphy of the LSSF are in agreement with the midden record, and all three reflect greater effective moisture during glacial times compared to today. Climatic limits associated with the modern distributions of plant species seen in other Pleistocene midden records from the Sonoran Desert (Van Devender, 1990) suggest that the increase in effective moisture was likely due to both cooler summers and wetter winters.

The added value of a "semi-continuous" pollen stratigraphy from LSSF is that it shows that woodland/chaparral communities detailed in our midden record were sustained at desert elevations continuously throughout the mid-to-late Wisconsin. None of the millennial (suborbital) scale variability identified in the ice core and marine sediment records (for the Gulf of California see Keigwin and Jones, 1990; for the Santa Barbara Basin see Kennett and Ingram, 1995; Behl and Kennett, 1996; Cannariato and Kennett, 1999) caused climatic changes sufficiently large to cause major detectable oscillations between woodland/chaparral and desertscrub assemblages in the midden series. This somewhat constrains the magnitude of the regional climatic changes associated with global-scale millennial-scale variability (Dansgaard-Oeschger and Heinrich Events).

The nearest comparable packrat midden series is at Cataviña, ~150 km south of the SSPM midden sites (Fig. 1), and is characterized by rich chaparral assemblages at 640–680 m during the glacial period up to ~12,000 cal yr BP (Wells, 1986; Van Devender, 1990; Peñalba and Van Devender, 1997; Peñalba and Van Devender, 1998; Betancourt et al., unpublished data). The persistence of conifers and chaparral elements into the early Holocene is confirmed by a midden from ~780 m on the southwestern piedmont of the Sierra San Francisco, another 300 km south of Cataviña (Rhode, 2002; Fig. 1). The midden records from the SSPM and Cataviña show that chaparral/woodland that included desert elements extended down to at least 640 m elevation in these areas during the glacial period. A recent midden survey along the eastern escarpment of the Sierra Juárez, 110 km north of the SSPM midden sites, produced 80 middens between 150 and 300 m, a third of which contain *Juniperus californica*. Dates and analyses are pending, but this suggests that there were practically no areas of pure desert vegetation (i.e., without conifers or chaparral elements) in Baja California north of 27°N during the late glacial period. High percentages of Taxodiaceae–Cupressaceae–Taxaceae pollen in glacial-age sections of the DSDP-480 core in the Guaymas Basin (Byrne, 1982; Byrne et al., 1990) may therefore reflect the broadscale expansion of junipers across what are now desert elevations in Lower Colorado River Basin, Baja California, and the Coastal Plains of Sonora.

Unlike the Cataviña record, which shows a much more dramatic turnover of species associated with the glacial–interglacial transition, the SSPM record is characterized by the persistence of many desert species (see middle section of Fig. 3). This stability is comparable to our midden series from Joshua Tree National Park, CA (Holmgren et al., 2010). This is somewhat surprising given the comparable elevation and greater proximity of the SSPM to Cataviña (~150 km; 640–680 m elevation) than Joshua Tree National Park (~290 km; 950–1350 m elevation).

The disappearance or increased rarity of chaparral species (*Arctostaphylos*, *C. betuloides*, *Juniperus californica*, *P. californiarum*, and *P. tridentata*) and appearance of several Sonoran Desert elements (*A. greggii*, *Bursera*, *Brickellia*, *H. emoryi*, *S. chinensis*, *A. palmeri*, *K. californica*, *Verbesina*, and *Echinocereus*) at the end of the Pleistocene signal the onset of more xeric conditions. As in midden records from north of the Mexico–U.S. border, several xeric-adapted Sonoran Desert plants that are missing from late-glacial assemblages arrive quickly during the latest Pleistocene–early Holocene. The persistence of some desert species throughout the record, combined with the rapid arrival of several others during the glacial–interglacial transition, suggests close proximity to the chaparral-desert ecotone and immigration from nearby desert communities. These newly-arriving

xerophytic species are presumed to have been restricted to desert refugia in areas with relatively mild conditions along the Coastal Plains of Sonora, southern Baja California (e.g., Vizcaino Desert) and the low-lying areas adjacent to the northern Gulf of California during the last glacial period, and later dispersed northward and to higher elevations following the advent of warmer temperatures in the early Holocene (Wells, 1977; Van Devender and Burgess, 1985; Betancourt, 1990; Van Devender, 1990; Van Devender et al., 1994; Holmgren et al., 2006). The low elevation, aridity, and high summer temperatures of the region surrounding the northern Gulf of California make it a particularly likely candidate for having harbored desert refugia during the last ice age. In addition, the >100-m drop in sea level during the Last Glacial Maximum would have increased the areal extent of this desert refugium significantly (Fig. 1). A key outstanding question, however, concerns the precise location and composition of this ice age refugium. The scarcity of suitable rock for midden preservation below ~400 m in most areas has hampered attempts to locate refugia. Likewise, the presence of *Juniperus californica* in numerous Pleistocene middens recently collected from 150 to 300 m along the eastern escarpment of the Sierra Juarez suggests that the modern Sonoran Desert likely assembled from many disparate populations of desert plants rather than from a few distinct refugia (Holmgren and Betancourt, work in progress).

Another pattern seen in the record in the late Pleistocene–early Holocene is the arrival or increasing abundance of C_4 grasses and summer-flowering annuals, signaling the onset of monsoonal precipitation (Fig. 4). In the SSPM these species include *Boerhavia*, *B. barbinodis*, *B. barbata*, *B. curtipendula*, *D. californica*, *Enneapogon*, *K. californica*, and *Setaria*. Of the above species, *Boerhavia*, *D. californica*, and *Setaria* are present during the full glacial, but become much more common after 13,585 cal yr BP. This is also the time when *B. curtipendula*

Figure 4. Plant macrofossil abundance through time for C_4 grasses and summer-flowering annuals.

and *K. californica* first appear in the record. The first appearance of *B. barbata* is somewhat later at 11,390 cal yr BP, followed by the appearance of *B. barbinodis* and *Enneapogon* at 8285 cal yr BP. It should be noted that Van Devender et al. (1990) argue that many of the above species are not true summer obligates, but may also flower in the fall if there is sufficient rainfall, or in the spring if it is warm and moist. We acknowledge that some of these species do occasionally respond opportunistically to rainfall outside of summer. The presence of only a few C_4 grasses and summer-flowering annuals at low abundances prior to 13,585 cal yr BP suggests that these species were either responding opportunistically to rainfall in seasons other than summer or that there was some summer precipitation during this period, but at a level insufficient to support the greater number and abundance of these species seen later. On the other hand, given the increase in C_4 grasses and summer-flowering annuals beginning around 13,585 cal yr BP, along with their central tendency to flower in summer, we think it is unlikely that the entire suite of species seen at this time was simply responding opportunistically to fall–spring rainfall.

Although moisture from the monsoon is less abundant in the study area than in southern Baja California, it contributes up to 50% or more of the annual total and is critical to this extremely arid region. Based on the increased abundances or new arrivals of C_4 grasses and summer-flowering annuals discussed above, our record suggests that monsoon onset in northeastern Baja California occurred later than in the Puerto Blanco and Tinajas Altas Mountains of southern Arizona, at approximately the same time as in the Whipple and Butler Mountains of Southern California and Arizona ~13,000 cal yr BP (Van Devender et al., 1990), but earlier than our site further to the north in Joshua Tree National Park at ~11,000 cal yr BP (Holmgren et al., 2010). This most likely reflects the relative proximity of these sites to the core monsoon region in the Sierra Madre Occidental.

Mitchell et al. (2002) argue that today the northward progression of sea surface temperatures >26°C in the Gulf of California is critical for the northward advance of monsoonal rains up the Gulf and into the Southwest, and that SSTs (>29°C) in early July are a good predictor of wet summers in Arizona. Based on this observation and temperature proxies in deep sea cores DSDP 480 and JPC 56 on either side of the Guaymas Basin (Fig. 1), Barron et al. (2005) suggest that the central Gulf may not have warmed sufficiently to support monsoonal rains in the northern Gulf and into Arizona until after ~6200 cal yr BP. The regular appearance of C_4 grasses and summer-flowering annuals since 13,600 cal yr BP in our record, indicative of summer rainfall equivalent to modern (JAS average of ~80–90 mm), casts doubt on this claim.

Following the glacial–interglacial transition, Holocene vegetation communities remained essentially stable. Most species found at the SSPM midden sites were present by the early Holocene, and this period is marked by the arrival of only a few more xeric-adapted species in the mid to late Holocene. These arrivals likely reflect the ameliorization of winter temperatures as insolation during this season increased to modern values.

Conclusions

Our new midden series from northern Baja California fills a significant spatial gap in midden coverage for western North America and provides new insight into past vegetation and climate dynamics. Particularly notable trends in the record include the expansion down slope of California chaparral species during the late glacial indicating greater winter precipitation, the late glacial–early Holocene disappearance of chaparral species and rapid replacement by Sonoran Desert elements, the increased importance of C_4 grasses and summer-flowering annuals during the glacial–interglacial transition as the North American Monsoon became established, and the overall stability of vegetation communities during the Holocene. This record allows for a greater understanding of the timing and extent of past
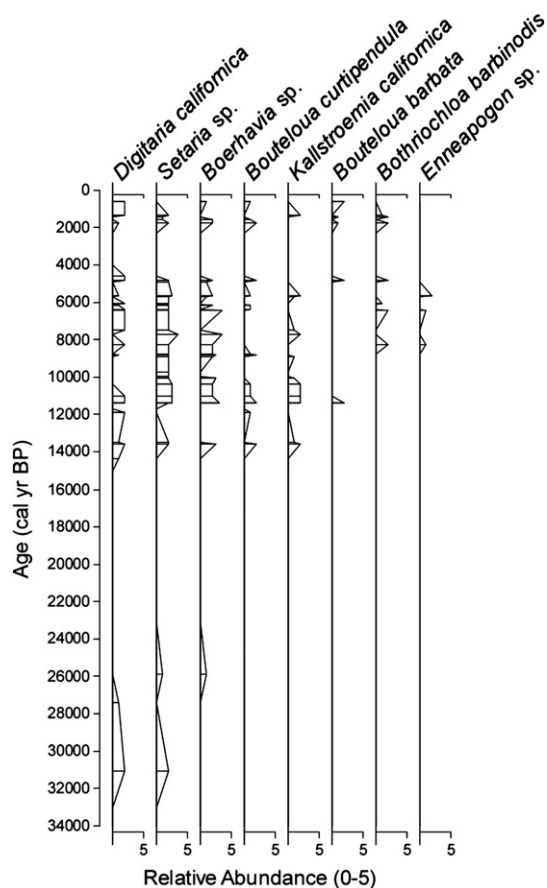
changes in vegetation and climate, and can provide a critical context for assessing modern variability and ecosystem change. For example, the overall stability of the vegetation recorded in the midden record for the Holocene contrasts markedly with changes projected for the next half century. Our record also suggests the potential for future midden studies in the area to further refine our knowledge of location of the California chaparral-desertscrub ecotone, community assembly patterns in the Sonoran Desert, and the dynamics of the North American Monsoon.

Acknowledgments

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