

A long-term vegetation history of the Mojave–Colorado Desert ecotone at Joshua Tree National Park

CAMILLE A. HOLMGREN,^{1*} and JULIO L. BETANCOURT^{2†} and KATE A. RYLANDER^{2†}

¹ Geography and Planning Department, Buffalo State College, Buffalo, New York, USA

² US Geological Survey Research Project Office, Water Resources Division, Tucson, Arizona, USA

Holmgren, C. A., Betancourt, J. L. and Rylander, K. A. A long-term vegetation history of the Mojave–Colorado Desert ecotone at Joshua Tree National Park. *J. Quaternary Sci.*, (2009). ISSN 0267-8179.

Received 8 December 2008; Revised 21 May 2009; Accepted 21 May 2009

ABSTRACT: Thirty-eight dated packrat middens were collected from upper desert (930–1357 m) elevations within Joshua Tree National Park near the ecotone between the Mojave Desert and Colorado Desert, providing a 30 ka record of vegetation change with remarkably even coverage for the last 15 ka. This record indicates that vegetation was relatively stable, which may reflect the lack of invasion by extralocal species during the late glacial and the early establishment and persistence of many desert scrub elements. Many of the species found in the modern vegetation assemblages were present by the early Holocene, as indicated by increasing Sørensen's Similarity Index values. C₄ grasses and summer-flowering annuals arrived later at Joshua Tree National Park in the early Holocene, suggesting a delayed onset of warm-season monsoonal precipitation compared to other Sonoran Desert and Chihuahuan Desert localities to the east, where summer rains and C₄ grasses persisted through the last glacial–interglacial cycle. This would suggest that contemporary flow of monsoonal moisture into eastern California is secondary to the core processes of the North American Monsoon, which remained intact throughout the late Quaternary. In the Holocene, northward displacement of the jet stream, in both summer and winter, allowed migration of the subtropical ridge as far north as southern Idaho and the advection of monsoonal moisture both westward into eastern California and northward into the southern Great Basin and Colorado Plateau. Copyright © 2009 John Wiley & Sons, Ltd.



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KEYWORDS: packrat middens; Pleistocene; Holocene; Joshua tree; juniper.

Introduction

Packrat midden research has made significant contributions to our general knowledge of the vegetation history of semi-arid North America, and has provided key insight into environmental and climatic history and biogeographical patterns. For example, the macrofossil assemblages preserved in midden chronologies have been used to investigate past vegetation communities (see regional summaries in Betancourt *et al.*, 1990), to reconstruct plant migrational patterns and pacing (Jackson *et al.*, 2002, 2005; Lyford *et al.*, 2003; Norris *et al.*, 2006), to infer millennial-scale variability in plant function from morphological and biological traits (Van de Water *et al.*, 1994, 2002; Hunter *et al.*, 2001), and to quantify past changes

in climate and evaluate their effects on shifting plant distributions (Thompson *et al.*, 1999; Arundel, 2002; Sharpe, 2002; Norris *et al.*, 2006; Holmgren *et al.*, 2007).

In addition to these scientific applications, the midden record can provide historical baselines helpful in managing natural areas. An important need is detailed knowledge about the long-term history and relative stability of the flora and vegetation in protected areas such as national parks, monuments and reserves, some of which are now being enveloped and impacted by exurban growth. One such place is Joshua Tree National Park (JTNP), which is imbedded in a region of eastern California that is experiencing unprecedented development (Stamos *et al.*, 2004; Hammer *et al.*, 2007; Syphard *et al.*, 2007), accelerated nitrogen deposition drifting in from Los Angeles smog (Allen *et al.*, 2007), and invasions by non-native grasses and other species that are increasing fire occurrence in the desert (Brooks and Matchett, 2006; Brooks and Minnich, 2006).

It is in this context of profound and contemporary ecological changes that we now provide a vegetation history of JTNP based on plant macrofossil analyses of 38 fossil packrat

*Correspondence to: C. A. Holmgren, Geography and Planning Department, Buffalo State College, 1300 Elmwood Avenue, Buffalo, NY 14222, USA.
E-mail: holmgrca@buffalostate.edu

†The contributions of J. Betancourt and K. Rylander to this article were prepared as part of their official duties as United States Federal Government employees.

middens that span the last 30 ka. Specific issues we addressed were: (1) the extent of floristic displacements during the last glacial period; (2) the degree of species persistence from glacial to interglacial, the timing of species departures and arrivals, and the impact of natural invasions as JTNP accumulated new species from the south during the Holocene; and (3) the long-term history of summer rainfall at JTNP, which today lies at the western limits of the North American Monsoon and receives almost half of its annual precipitation during July through September.

Study area

Physiographic setting

Joshua Tree National Park is located at the eastern end of the Transverse Ranges physiographic province, which stretches from Point Arguello west of Santa Barbara, California, more than 520 km eastward to the Eagle Mountains in the southeast corner of JTNP (Fig. 1). The park contains several mountain ranges including the Little San Bernardino Mountains in the southwest, the Cottonwood, Hexie and Pinto Mountains in the centre, and the Eagle and Coxcomb Mountains in the east (Fig. 2). Pockets of Precambrian Pinto Gneiss are exposed in the study area, although much of this has been intruded by Mesozoic plutons including the Palms Granite, Gold Park

Diorite, Queen Mountain monzogranite and White Tank monzogranite (Trent, 1984; Covington, 2003). Weathering along joint systems within the White Tank monzogranite produced the large rock piles and inselbergs that characterise much of the northern part of JTNP, including Indian Cove, Jumbo Rocks, Skull Rock, Split Rock and the Wonderland of Rocks (Trent, 1984), from which all middens in this study except Mastodon Peak 1B were collected. Quaternary alluvial sediments commonly blanket the lower valleys. The park is bounded to the north by the Pinto Mountain Fault, which runs approximately parallel to State Highway 62, and to the south by the E–W trending Blue Cut Fault (Trent, 1984). The nearest forested mountains are the San Bernardino Mountains to the west, where a series of moraines on Mount San Gorgonio, the highest peak at ~3450 m, correspond to the southernmost limit of glaciation in the western Cordillera of North America, including the surprisingly recent advances between 9 and 5 ka (Owen *et al.*, 2003).

Climate

Mean monthly air temperature and total monthly precipitation values spanning the period 1935–2005 were obtained from the National Oceanic and Atmospheric Administration's National Climatic Data Center for Twentynine Palms, California (602 m), located just north of the study area. The average annual temperature at Twentynine Palms is 19.9°C, with average

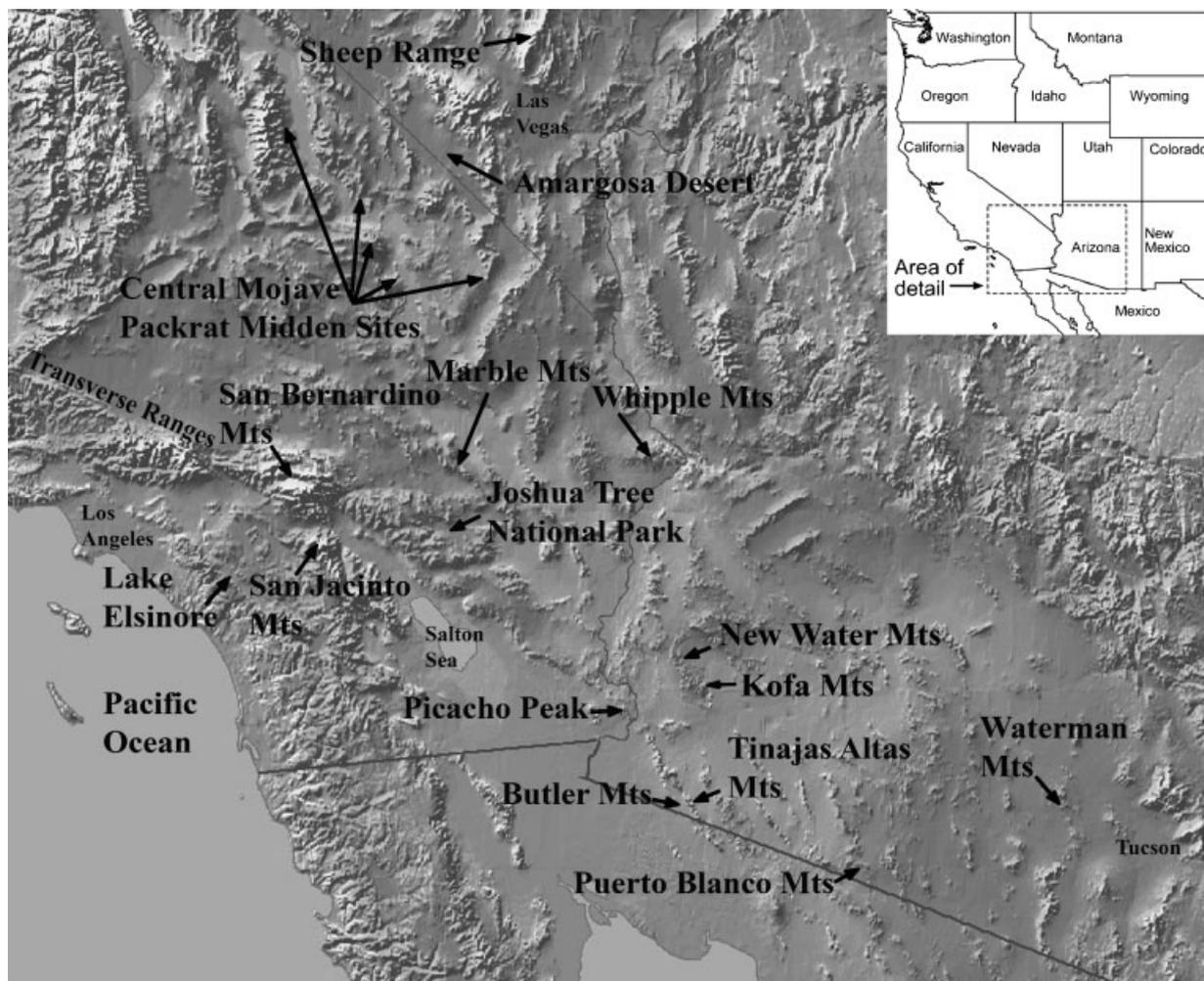


Figure 1 Map of study area showing the location of sites mentioned in the text

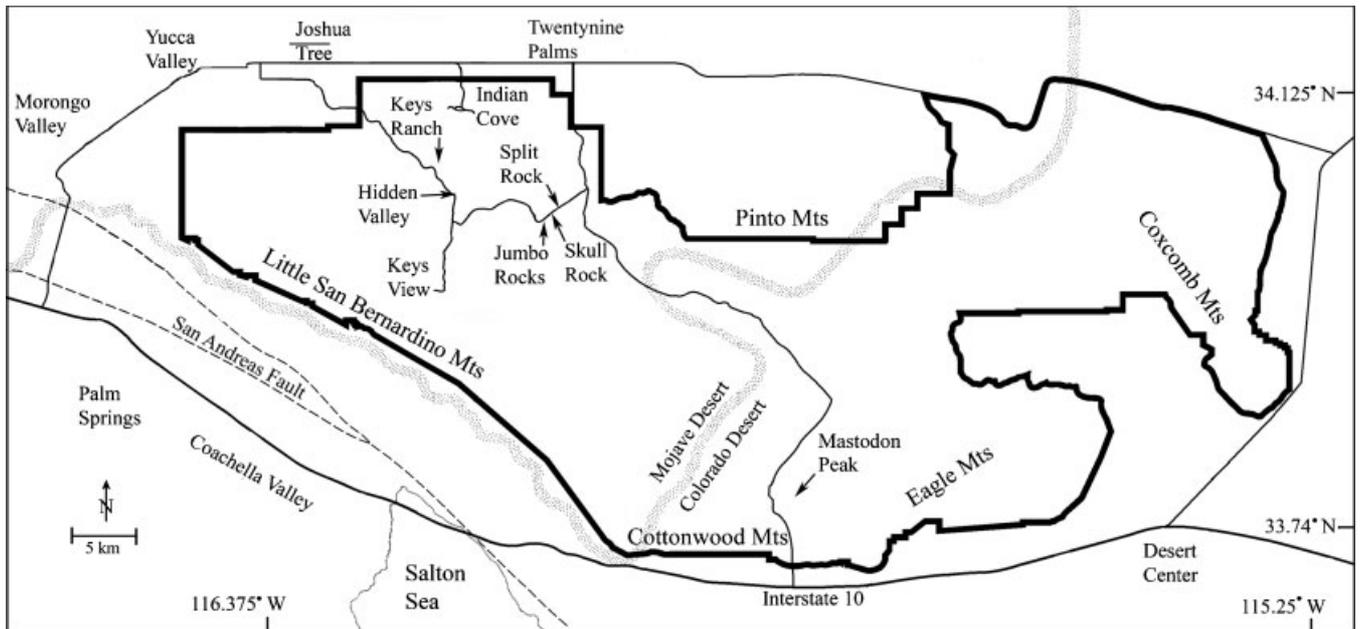


Figure 2 Map of Joshua Tree National Park showing the location of midden sites

monthly temperatures ranging from 9.6°C in January to 31.4°C in July. Annual precipitation averages 110.0 mm and varies seasonally throughout the year (Fig. 3(a)). The driest conditions occur during the arid foreshummer from April through June (4.9% of annual precipitation), followed by summer precipitation in July through September (40.7% of annual precipitation), and then variable fall and winter precipitation from October through March (54.4% of annual precipitation). Summer precipitation in the form of convective thunderstorms results from the occasional penetration of moisture associated with the North American Monsoon into southeastern California (Tubbs, 1972; Adams and Comrie, 1997; Higgins *et al.*, 2004; Vera *et al.*, 2006). Winter precipitation, on the other hand, results from large frontal systems moving inland from the north Pacific Ocean as expansion of the Aleutian Low shifts the Pacific storm track southward (Pyke, 1972).

Interannual- and decadal-scale variability in cool season (October–April) precipitation in both the Sonoran and Mojave Deserts is modulated by both El Niño–Southern Oscillation (ENSO) (Cayan *et al.*, 1999; McCabe and Dettinger, 1999; Hereford *et al.*, 2006) and the Pacific Decadal Oscillation (PDO) (Mantua and Hare, 2002). The relationship to winter precipitation in the southwestern USA is strengthened when the warm or cold phases of ENSO and PDO coincide and weakened when they are out of phase. These patterns, however, can vary subregionally (Brown and Comrie, 2002) and, even in neutral ENSO years, the PDO tends to modulate winter precipitation variability (Goodrich, 2004). This close correspondence of winter rainfall to both ENSO and PDO can be seen in time series of spring annual bloom anomalies inferred from herbarium specimens collected over the 20th century, with moderate decadal-scale persistence and synchrony in either good or bad wild flower years across both the Mojave and Sonoran Deserts (Bowers, 2005).

Interannual and decadal-scale variability in warm season precipitation (July–September) is less well understood. JTNP lies near the westernmost extension of the North American Monsoon, and is also affected by dissipating tropical cyclones from the eastern North Pacific. Monsoonal rainfall variability at JTNP is similar to southwestern Arizona at interannual timescales, as indicated by the correlation in August precipitation (the month with the greatest monsoonal rainfall) between

Twentynine Palms, CA, and Yuma, AZ, from 1950 to 1995 ($r^2 = 0.32$, $P = 0.0001$) using data from the National Climatic Data Center (www.ncdc.noaa.gov/oa/ncdc.html). Although not particularly strong, this correlation is probably reasonable given the small-scale, localised nature of convective monsoonal storms. On the other hand, monsoonal rainfall exhibits little decadal-scale persistence, although there is a slight tendency for runs of several consecutive dry summers, most notably in the years from 1988 to 1996 (Hereford *et al.*, 2006) (Fig. 3(b)). This interval was characterised by wet summers across the Great Plains and New Mexico, and dry summers from western Arizona/southern California north into the Intermountain West, and may be instructive for identifying persistent large-scale circulation features that contribute to summer drought at JTNP. For example, relatively wet conditions within the North American Monsoon are often associated with the presence of moist low-level southerly or southeasterly flow linked to the passage of easterly wave troughs across western Mexico and the presence of strong upper-level anticyclonic circulation over the central USA, while drier conditions are related to upper-level anticyclonic circulation located over the west coast of the USA (Higgins *et al.*, 2004; Vera *et al.*, 2006).

Vegetation

JTNP encompasses parts of both the Mojave and Colorado Deserts. The Colorado Desert is generally considered the western extension of the Sonoran Desert and corresponds to the Lower Colorado Valley subdivision of the Sonoran Desert (Shreve, 1951), later modified as the Colorado subdivision of the Sonoran Desert (Turner and Brown, 1982). Although overlap in the ranges of several indicator species makes sharp delineation of the boundary between the Mojave Desert and the Colorado Desert difficult (Turner, 1994), Holland (1986) recognised a general transition between communities of the two within JTNP at roughly 910–1210 m. Vegetation in much of the northern part of JTNP (including the Jumbo Rocks, Skull Rock, Split Rock, Hidden Valley and Keys Ranch midden sites from 1247 to 1357 m) is most similar to the Joshua Tree Series of

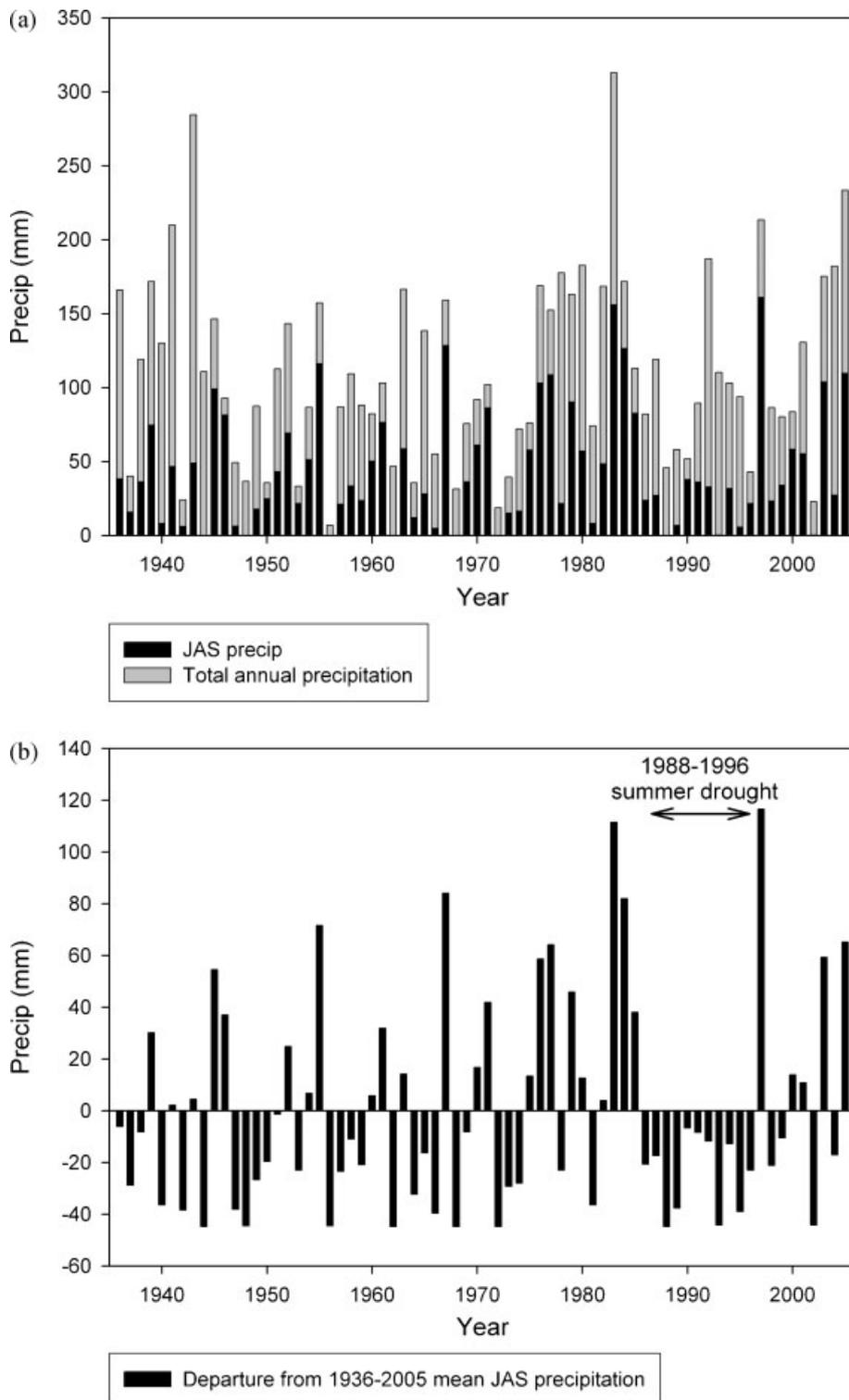


Figure 3 Precipitation data for Twentynine Palms, CA. (a) Annual precipitation values for 1936–2005. Summer monsoon (July–August–September, JAS) precipitation is shown in black and the total annual value is shown in grey. (b) Departure of JAS precipitation from 1936 to 2005 mean showing interannual variability in warm season rainfall and 1988–1996 summer drought

the Mojave Desertscrub community with some Great Basin Conifer Woodland elements (Turner, 1994). For a listing of all plant taxa mentioned in the text and figures see supporting information Table 1. Vegetation here is dominated by *Acacia greggii* (catclaw acacia), *Ephedra* spp. (Mormon tea), *Eriogonum fasciculatum* (California buckwheat), *Hymenoclea salsola* (cheesebush), *Lycium* spp. (box thorn), *Nolina parryi* (bear-grass), *Opuntia echinocarpa* (silver cholla), *Peucephyllum schottii* (pygmy cedar), *Prunus fasciculata* (desert almond),

Simmondsia chinensis (jojoba), *Yucca brevifolia* (Joshua tree), *Yucca schidigera* (Mojave yucca), and scattered *Juniperus californica* (California juniper), *Pinus californiarum* (California single-leaf pinyon) and *Quercus cornelius-mulleri* (Muller's oak) individuals. Other vegetation includes a variety of shrubs and herbs, including *Amsinkia* sp. (fiddleneck), *Artemisia ludoviciana* (sagebrush), *Astragalus* spp. (milkvetch), *Atriplex* spp. (saltbush), *Brickellia* spp. (brickellbush), *Castilleja angustifolia* (desert paintbrush), *Coleogyne ramosissima* (black-brush), *Chrysthamnus viscidiflorus* (rabbitbush), *Cryptantha*

Table 1 Radiocarbon dates and site locations of rodent middens

Midden designation	Latitude (°N)	Longitude (°W)	Elevation (m)	Slope aspect	¹⁴ C Age (a BP)	SD	Lab code	Calibrated 2σ age range (a BP)	Calibrated age midpoint	Material dated
Indian Cove 20	34.08342	116.13945	945	SW	1 225	15	30811	1073–1236	1 155	Faecal pellets
Hidden Valley 84A	34.02007	116.16373	1290	SW	1 620	25	30779	1416–1560	1 490	Faecal pellets
Jumbo Rocks 53	33.99117	116.06755	1340	SE	1 695	15	30816	1543–1690	1 615	Faecal pellets
Skull Rock North 41	33.99764	116.06329	1330	S	1 725	25	30795	1563–1702	1 635	Faecal pellets
Skull Rock North 40B	33.99767	116.06260	1325	S	1 920	25	30794	1820–1925	1 875	Faecal pellets
Keys Ranch 1A	34.02517	116.14838	1285	E	2 045	20	30818	1933–2107	2 015	Faecal pellets
Jumbo Rocks North 74	33.99450	116.07028	1349	SSE	2 065	25	30790	1950–2117	2 035	Faecal pellets
Indian Cove E 90	34.08537	116.13975	958	S	2 215	15	30813	2153–2318	2 235	Faecal pellets
Hidden Valley W 94B	34.01030	116.16652	1271	SW	2 210	25	30781	2151–2318	2 235	Faecal pellets
Hidden Valley W 30	34.01117	116.16746	1274	SW	3 730	25	30777	3985–4151	4 070	Faecal pellets
Jumbo Rocks 42	33.99483	116.06700	1318	N	3 865	25	30789	4162–4411	4 285	<i>Prunus</i> seed
Malapai Hills 1A	33.93265	116.07510	1090	S	3 885	45	AA64693	4157–4422	4 290	Faecal pellets
Jumbo Rocks 39C	33.99367	116.06840	1352	SSW	4 155	25	30786	4583–4825	4 705	<i>Prunus</i> seed
Jumbo Rocks North 77	33.99548	116.07012	1350	NW	4 300	25	30791	4830–4958	4 895	<i>Prunus</i> seed
Jumbo Rocks 39D	33.99367	116.06840	1352	SSW	4 435	25	30787	4881–5275	5 080	<i>Prunus</i> seed
Jumbo Rocks 39E	33.99367	116.06840	1352	SSW	4 435	25	30788	4881–5275	5 080	<i>Prunus</i> seed
Mastodon Peak 1B	33.99863	116.05282	1320	W	4 655	55	AA64695	5293–5581	5 440	Faecal pellets
Hidden Valley W 85B	34.01051	116.16538	1247	NW	4 735	25	30780	5329–5582	5 455	Faecal pellets
Jumbo Rocks 26	33.99070	116.05410	1313	NE	4 885	20	30815	5591–5648	5 620	Faecal pellets
Keys Ranch 97A2	34.02405	116.15535	1282	W	5 165	25	30793	5687–5989	5 838	<i>Prunus</i> seed
Keys Ranch 97A1	34.02405	116.15535	1282	W	6 010	20	30819	6787–6930	6 860	<i>Prunus</i> seed
Hidden Valley W 95B	34.01099	116.16782	1276	N	6 535	20	30810	7423–7478	7 450	Faecal pellets
Hidden Valley 80A	34.01519	116.16275	1259	NNE	7 040	25	30807	7799–7941	7 870	<i>Prunus</i> seed
Malapai Hills 1B	33.93265	116.07510	1090	S	7 110	50	AA64694	7837–8019	7 930	Faecal pellets
Hidden Valley 80B	34.01519	116.16275	1259	NNE	7 695	30	30778	8418–8542	8 480	Faecal pellets
Keys Ranch 1B	34.02517	116.14838	1285	E	7 905	30	30792	8599–8972	8 785	Faecal pellets
Jumbo Rocks 39B	33.99367	116.06840	1352	SSW	7 955	30	30785	8649–8986	8 820	Faecal pellets
Hidden Valley W 85A	34.01051	116.16538	1247	NW	8 185	25	30809	9027–9256	9 140	Faecal pellets
Jumbo Rocks 22	33.99250	116.05905	1325	ESE	8 720	30	30814	9552–9884	9 720	<i>Nolina</i> stem
Jumbo Rocks North 68	33.99388	116.06843	1357	SE	8 815	30	30817	9698–10123	9 910	<i>Nolina</i> stem
Hidden Valley 80C	34.01519	116.16275	1259	NNE	9 185	30	30808	10247–10480	10 365	<i>Prunus</i> seed
Indian Cove 16	34.09938	116.17263	1028	S	9 275	35	30782	10298–10572	10 435	Faecal pellets
Indian Cove 49	34.08492	116.43080	952	SSE	9 300	40	30783	10299–10648	10 475	Faecal pellets
Hidden Valley 62	34.01635	116.16383	1280	S	9 710	35	30776	10892–11222	11 055	Faecal pellets
Jumbo Rocks 39A	33.99367	116.06840	1352	SSW	12 015	45	30784	13766–13991	13 880	Faecal pellets
Hidden Valley 1977	34.03000	116.17000	1280	SW	12 790	750	no data	13982–15996	14 990	<i>Juniperus</i> stem
Indian Cove 60B	34.09637	116.15250	930	W	29 260	420	30812	33718–34987	34 355	Faecal pellets
Split Rock East 38A	34.00986	116.05497	1337	W & E/Ravine	>47 200	n/a	30796	>47200	>47 200	Faecal pellets

sp., *Encelia farinosa* (brittlebush), *Hibiscus denudatus* (rose-mallow), *Lotus rigidus* (desert rock pea), *Phacelia* sp. (scorpion-weed), *Phoradendron californicum* (desert mistletoe), *Rhus trilobata* (skunkbrush), *Salvia columbariae* (chia), *Sphaeralcea* spp. (globemallow), *Thamnosia montana* (turpentine broom); cacti including *Echinocereus triglochidiatus* (hedgheg cactus), *Opuntia basilaris* (beavertail cactus), *Opuntia ramosissima* (pencil cactus) and *Opuntia* spp. (prickly-pear); and grasses including *Achnatherum hymenoides* (Indian ricegrass), *Elymus* cf. *elymoides* (squirreltail), *Sporobolus airoides* (alkalai sacaton), and invasive *Bromus tectorum* (cheat grass) and *Bromus madritensis* ssp. *rubens* (red brome). At the somewhat lower elevation Indian Cove site (930–1028 m) along the northern periphery of the park, vegetation is more closely allied with the Creosotebush Series of the Mojave Desertscrub (Turner, 1994). Here *Larrea tridentata* (creosote bush), *Ambrosia dumosa* (burro-weed), *Simmondsia chinensis* and *Brickellia* spp. become increasingly important elements and *Juniperus californica*, *Quercus turbinella*, *Lycium*, *Nolina* and *Peucephyllum schottii* are rarer. Other species found at this location include *Nicotiana trigonophylla* (desert tobacco), *Condalia globosa* (bitter condalia), *Ferocactus cylindraceus* (barrel cactus) and *Prosopis glandulosa* var. *torreyana* (honey mesquite). This lower-elevation site exhibits increased similarity with vegetation in the lower and warmer Colorado Desert in the southeastern part of the park, although notable

distinctions exist between the two. The Colorado Desert below ~910 m is characterised by increased dominance of *Larrea tridentata* and *Prosopis glandulosa* var. *torreyana*, and the presence of *Opuntia bigelovii* (teddy-bear cholla), *Cercidium* spp. (palo verde), *Fouquieria splendens* (ocotillo), *Justicia californica* (chuparosa) and *Psoralea spinosa* (smoke tree). Due to lack of suitable and accessible rock to the south, collection of middens was constrained to the northern part of JTNP with the exception of a single midden collected near the Cottonwood Visitor Center (Mastodon Peak 1B).

One of the principal management questions is the degree to which fire has played an ecological role along the elevation/vegetation gradient at JTNP. Except at the highest elevations, the natural vegetation is characterised by barren ground in between desert shrubs and cacti, which have little adaptation to fire. This has changed with invasion by non-native Mediterranean grasses such as *Bromus madritensis* var. *rubens*, *Bromus tectorum* and *Schismus*, which tend to connect the woodier fuels, especially following wet falls and early winters, and recover quickly after fire. With each subsequent fire the native plants vanish but these invasive grasses thicken and expand, fuelling ever larger and more frequent wildfires, inducing what has been called the 'grass–fire cycle'. Prior to 1965, fire records at the park suggest that most lightning-caused fires, which happened in May through September, seldom spread more than a few tens of metres from the strike. With the shift to a positive

PDO Index and wetter winters, *Bromus madritensis* var. *rubens* spread dramatically and began fuelling large fires in both the Mojave and Sonoran Deserts. At JTNP, fires measuring in the thousands of acres burned in 1979, 1995, 1999 and 2006 (<http://www.nps.gov/jotr/naturescience/fireregime.htm>). The increase in fire size and frequency could transform JTNP vegetation in a matter of decades.

Methods

Midden collection and processing

We collected more than 100 middens from upper desert (930–1357 m) elevations to reconstruct changes in vegetation since the Last Glacial Maximum and selected 38 middens for radiocarbon analysis. Most of the middens were sampled by CAH and JLB in April 2006, but three (Malpai Hills #1A and 1B and Mastodon Peak 1B) were sampled by JLB in April 2005, and another (Hidden Valley #1977; formerly referred to as Split Rock #1) by Tom Van Devender in 1977. A minimum of 500 g of material was collected, wherever possible leaving enough material *in situ* to permit resampling. A chisel and rock hammer were used to remove the outer midden rind of contaminants, and splits made along bedding planes to separate different layers if necessary. 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 first inspected and any remaining rind was removed to rid the sample of modern contaminants. Next, middens were washed and dried, and plant macrofossils (e.g. twigs, leaves, seeds, flowers and fruits) were sorted and identified by comparison to modern reference material. Macrofossils were then quantified using a relative abundance scale of 0 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 ≥ 200 fragments. An interesting check on the temporal integrity of the middens is the absence of non-native species in the macrofossil assemblages. Despite being widespread and dominant enough to drive extensive fires across JTNP and surrounding areas, for example, neither *Bromus tectorum* nor *Bromus madritensis* ssp. *rubens* were found in any of the middens.

Material for radiocarbon dating (rodent faecal pellets or plant macrofossils) was pretreated at California State University, Long Beach, and measured at the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. The Calib 5.0.2 Intcal04 calibration curve (Stuiver and Reimer, 1993) was used for samples <21 ¹⁴C ka BP and the CalPal-2007-Hulu curve was used for samples >21 ¹⁴C ka BP (www.calpal.de). For plotting purposes, we selected the midpoint of the calibrated 2σ age range. Dates are reported herein as the midpoint of calibrated age ranges (Table 1).

Macrofossil identification

Pinyon needles from the middens were identified based on the number of needles per fascicle, needle diameter, and the number of resin canals and stomatal rows. *Pinus californiarum*, the most common pinyon in the middens and the one present at JTNP today, is characterised by fascicles with a single stout (1.2–1.6 mm in diameter) needle with thickened sclerophyll layers and the presence of 8–16 resin canals and 13–18

stomatal lines. In contrast, the other single-needled pinyon in the region, *Pinus monophylla* (single-leaf pinyon), has 2–7 resin canals and 17–30 stomatal lines (Bailey, 1987; Cole *et al.*, 2008). *Pinus juarezensis* (Sierra Juárez pinyon) is a five-needled pinyon that occurs from the San Jacinto Mountains of southern California, 50 km southwest of JTNP, into the Sierra Juarez and Sierra San Pedro Martir of Baja California. In the San Jacinto Mountains, *Pinus juarezensis* hybridises with the one-needled *Pinus californiarum* to produce hybrid swarms of trees that bear one to five needles per fascicle (Lanner, 1974; Lanner and Van Devender, 1998). In the middens, *Pinus juarezensis* was identified based on comparison to modern reference material obtained from the University of Arizona herbarium and by the presence of two- and three-needled fascicles, two resin canals, 14–20 stomatal rows, gracile needles, small stomatal size and thin shells.

Three species of junipers (*Juniperus grandis*, *J. californica* and *J. osteosperma*) occur today in southern California (Adams, 1993; Baldwin *et al.*, 2002; Adams *et al.*, 2006), and any of three could have grown at JTNP in the past. *J. grandis* (Sierra juniper; syn. *J. occidentalis* var. *australis*; see Adams *et al.*, 2006) occurs along the eastern slope of the Sierra Nevada south of 40.5 °N, as far east as the Panamint Mountains in Nevada and as far south as the San Bernardino Mountains, just west of JTNP. This long-lived tree grows scattered with other conifers from 1250 to 2800 m elevation and commonly yields sensitive ring-width chronologies (Miller *et al.*, 2005). The smaller Utah juniper, *J. osteosperma*, grows throughout the Colorado Plateau and Great Basin, extending north into the Wyoming Basins and southern Idaho, and southwest into California to the northern piedmont of the San Bernardino Mountains. In California, Utah juniper grows between 1300 and 2600 m. *J. californica* is the only juniper growing today in JTNP. It grows primarily in California between 750 and 1600 m, but also extends into southern Nevada, western Arizona and Baja California (Adams, 1993). Field identification can be difficult for these junipers (e.g. *J. californica* vs. *J. osteosperma*) and may be confounded in hybrids (e.g. *J. osteosperma* × *occidentalis*) (Vasek, 1966; Adams, 1993; Terry *et al.*, 2000).

For field identification of North American junipers, numerous characters have been used either separately or in combination in various dichotomous keys. These morphological characters have included bark colour and texture, aril colour, cone colour and size, presence or absence of abaxial leaf glands, leaf gland shape or size, presence or absence of teeth along leaf margins, whip gland characters, general tree phenology and growth habit, to name just a few (Adams, 1993; Baldwin *et al.*, 2002). Historically, the separation of *J. californica* from *J. osteosperma* and the former *Juniperus occidentalis* has been extremely difficult using these morphological characters alone (Adams *et al.*, 2006). Analysis of various juniper species' volatile leaf oils and wood oils, however, has provided a point of separation for distinguishing the three species. For example, terpenoids have been useful in identifying junipers with serrate margins to the species level (Adams, 2000a). Recent advances in DNA technology (including nrDNA, trnC and trnDNA) have complemented the morphological and essential oil data (Adams and Demeke, 1993; Adams, 2000b). Both DNA data (RAPDs) and leaf essential oils now show that *J. californica*, *J. osteosperma* and *J. grandis* are distinct entities.

If field identifications of southern California junipers are difficult, so much the worse for determination of juniper remains in middens. The midden material is usually abundant, consisting of hundreds of stem fragments and seeds. The assumption that all of the juniper remains in a single midden belong to one species is not justified, thus requiring careful

examination of most of the stems. The lack of standard macrofossil keys and protocols used by all midden researchers raises some legitimate questions about juniper identification, which is difficult in its own right. We offer the following guidelines for other researchers.

Branchlets covered by juniper's distinctive whorls of apiculate arrow-shaped leaves comprise possibly 95% of the recovered juniper material from JTNP. Because there is no suitable key for leaf characters in junipers, we set out to develop one using modern reference material for *J. californica*, *J. grandis* and *J. osteosperma* previously identified based on both field morphological characteristics and random amplified polymorphic DNA (RAPDs) and that had been used to redefine the systematics of the serrate leaf junipers of the western USA (Adams, 2000b). We also included two additional specimens of *J. occidentalis* var. *occidentalis* from herbarium sheets archived at the University of Arizona's Desert Laboratory.

Ten random stems from each of the modern species populations and from each of the 32 JTNP midden samples containing juniper were examined. The stems from JTNP were treated with reagent-grade chloroform to remove excess wax and dirt on the surface of the fossil specimens. Both modern and fossil junipers were examined under a Nikon SMZ-U binocular scope at 75× magnification for 10 different characteristics including stem width, leaf shape, presence/absence of visible stomata on the dorsal leaf surface, quality of leaf margin teeth, gland appearance (erupting or non-erupting), epidermal surface traits (lenticular vs. a mix of lenticular and polygonal cell shapes), the presence of small papillae or bumps in the stomatal area of the dorsal leaf surface, the presence of beading on the dorsal leaf surface, an estimate of primary vs. secondary twig growth, and seed length (supporting information Table 2). An eleventh character, whether the dorsal surface of the leaf sports a conspicuous gland, was later added in an attempt to further differentiate *J. osteosperma* (inconspicuous; Fig. 4(a)) from *J. californica* (conspicuous; Fig. 4(b)) as denoted by the *Flora of North America* (Adams, 1993). *J. occidentalis* has been split

into a northern variety, *J. occidentalis* var. *occidentalis*, and a southern variety, *J. grandis*, which occupies dry, rocky slopes in southern California, including the San Bernardino Mountains and the Sierra Nevada in western Nevada. Erupting glands are characteristic of *J. occidentalis* var. *occidentalis*, the northern variety of western juniper, whereas it is rarer in the other two species. Subsequent study by Adams notes that the leaf glands of *J. grandis* are usually not ruptured (www.juniperus.org/keys.html), although modern specimens used for this study did show that *J. grandis* occasionally had erupting glands, but not to the extent of that found in *J. occidentalis* var. *occidentalis*. Seed size among the three species was also suggestive as to species: *J. californica* produces seeds 5–7 mm in length, whereas those from *J. osteosperma* (seeds 4–5 mm length), *J. occidentalis* var. *occidentalis* and *J. grandis* (seeds 2–4 mm) are shorter (Adams, 1993).

In addition, several stems from both the modern reference material and fossil specimens from JTNP were coated with 30 nm of gold using a Hummer 6.2 sputtering device and examined using a Hitachi 3400N scanning electron microscope (SEM). An average of 10 branchlets per modern species population and 10 branchlets per fossil sample were observed on the SEM. Specimens were observed at various magnifications from 75× to 1000×. A Hitachi PC_SEM program was used to measure the length and width of stomata visible on the dorsal surfaces of both modern and fossil juniper leaves. These measurements were then used to calculate the area of individual stomata (see supporting information Table 3).

More than 3200 fossil juniper leaves and 1000 modern juniper leaves were observed for this study. We confirmed that *J. californica* was overwhelmingly the dominant juniper in the JTNP macrofossil record. It was identified in each of the 32 JTNP packrat midden samples based on a combination of characters including branchlet width, occurrence of spatulate, flattened leaves in addition to hooded or keel shaped leaves, the presence of conspicuous but non-erupting glands, and the existence of minute papillae on both the epidermal surface and

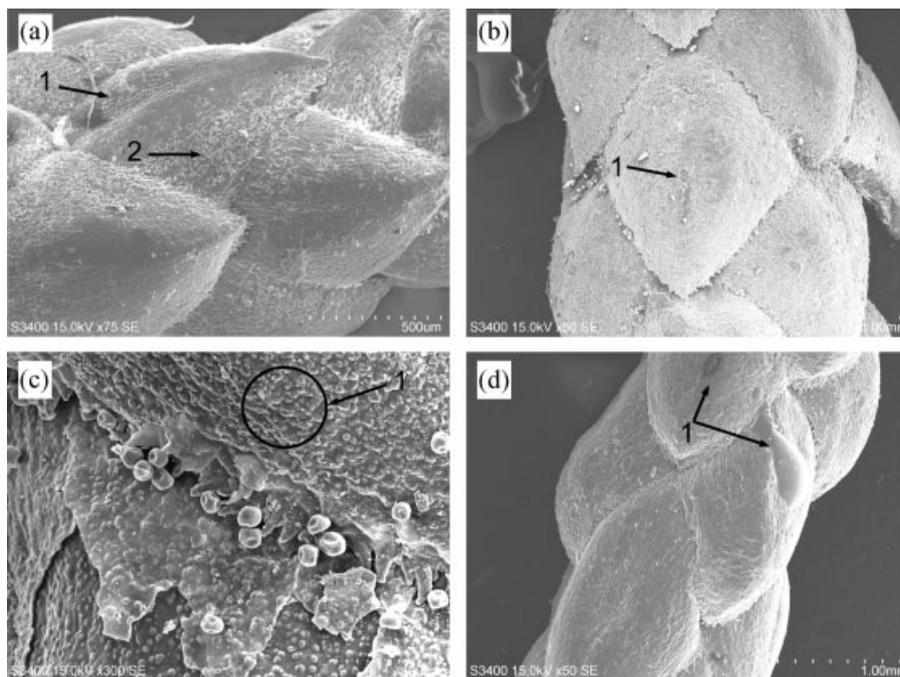


Figure 4 SEM images of juniper species. (a) *Juniperus osteosperma* stem with dorsal leaf surface lacking conspicuous gland (1). This species has minor surface roughness (2) that is irregular and 'low' compared to bumps on *Juniperus californica* (see panel c for comparison). (b) *Juniperus californica* stem with keel-shaped leaves and conspicuous but non-erupting gland (1) on dorsal leaf surface. (c) *Juniperus californica* showing minute surface papillae (1) on the epidermal surface. (d) *Juniperus grandis* with erupting glands (1) on dorsal surface of diamond shaped leaves

the bottom of the leaf near the stomata (Fig. 4(c)). The size (height), number and regularity of these bumps were distinctive to *J. californica*, with the overall leaf surface appearing quite rough even at 75× magnification. Although *J. grandis* exhibited some low bumps on some epidermal cells on its dorsal surface, they were quite 'low' in comparison to that of *J. californica* and occurred more prominently on the top half of the leaf. *J. osteosperma* also has some surface roughness on the leaf, but this is irregular and more nondescript.

The surface papillae of *J. californica* may represent an epidermal modification that actually reduces evapotranspiration by slowing the air that flows over the leaf (Adams, pers. comm.). Papillae near the stomata would also affect the amount of CO₂ flowing around and into the apertures. The thick leaves and heavy waxy covering would additionally reduce water loss. As Miller *et al.* (2005) noted for *J. occidentalis*, a highly cuticularised leaf morphology where stomata are located at the bottom and are covered by the adjoining leaf allows for maximum drought efficiency. A less defensible theory is that these papillae represent modifications of the epidermal cells wherein the papillae actually contain some form of leaf volatile oil as they do in other botanical families such as rice. *J. californica* is the only one of the three species known to produce leaf volatile oils (Adams, 1993). Indeed, two morphologically identical races of *J. californica* have been described based on differences in leaf oils alone (Vasek and Scora, 1967).

Virtually all of the fossil juniper leaves examined from JTNP exhibited non-erupting glands, with the exception of those from the Hidden Valley 1977 (14 990 a BP) and Jumbo Rocks 39A (13 880 a BP) middens. These stems had erupting glands visible on nearly every leaf surface. Stems with erupting glands comprised >50% of the juniper material in the 14 990 a BP sample, but only a few branchlets in the 13 880 a BP sample. Smaller twig diameter, diamond-shaped leaves, lack of papillae and the prevalence of erupting glands all indicate *J. occidentalis*-type (Fig. 4(d)). These fossils may represent either an incursion of the northern variety *J. occidentalis* var. *occidentalis* south into the JTNP region during the more mesic conditions of the late Pleistocene, or the occurrence of a Pleistocene variety of *J. grandis* in which erupting glands were more common than in modern populations. Because an incursion of *J. occidentalis* var. *occidentalis* would require a southward displacement of over 600 km, the latter explanation is much more parsimonious and we refer to our fossils as *J. grandis*.

Finally, our analysis of stomatal size revealed some disparities between modern and fossil juniper specimens. Although stomatal size varied among the juniper species examined, we found that fossil specimens generally had greater numbers of stomata on their dorsal surfaces, but these stomata were on average about 50% smaller than their modern counterparts (supporting information Table 3). Studies based on fossil and herbarium materials (Woodward, 1987; Van de Water *et al.*, 1994; Garcia-Amorena *et al.*, 2006) and growth chamber experiments (Royer *et al.*, 2001; Teng *et al.*, 2006) indicate that stomatal density declines with increasing CO₂ levels. We thus speculate that having fewer and larger stomata may be a response to higher atmospheric CO₂ levels since industrialisation.

Research over the past several decades has led to substantial revision of the taxonomy of scrub white oaks (*Quercus*, section *Quercus*) in California, with more attention now paid to growth habit, acorn morphology and variation in leaf vestiture. Within California most populations previously referred to as *Quercus turbinella* (shrub live oak) are now known as either *Q. john-tuckeri* (Tucker's oak; syn. *Q. turbinella* var. *californica*) or

Q. cornelius-mulleri. The majority of typical *Q. turbinella* populations occur farther to the east from Arizona to Texas and into northern Mexico, although a few populations occur along the eastern desert ranges of California near the Arizona border and along the eastern slopes of the Sierra San Pedro Juarez and Sierra San Pedro Martir in Baja California (Nixon and Steele, 1981; Nixon, 2002). The proximity of *Q. turbinella* populations in southern California to JTNP suggests that this species could have extended its range into the park during the past. Although both *Q. john-tuckeri* and *Q. cornelius-mulleri* are present at JTNP, *Q. cornelius-mulleri* is the common species at the midden sites today and was the only species identified in the middens. This species can be identified by leaves with dense, overlapping stellate trichomes on the lower surface that are microscopically fused into a ring or plate at the centre (Nixon and Steele, 1981). A few middens lacked diagnostic material (i.e. they contained only stem or acorn fragments or leaves with badly eroded hairs), so the presence of *Q. john-tuckeri* and/or *Q. turbinella* in the midden record cannot be completely ruled out.

Results

Radiocarbon dating

Middens from JTNP range in age from >47 200 to 1155 a BP (Table 1). Three middens (>47 200, 34 355 and 14 990 a BP) date from the full glacial period, although the midden at >47 200 a BP has an 'infinite' date, which should be considered a minimum age only. Thirty-five additional middens provide unusually even coverage for the late Pleistocene through the late Holocene, with only three temporal gaps greater than ~600 years. Eleven samples dating from 13 880 to 8480 a BP document changes associated with the glacial–interglacial transition, another 15 samples span the middle Holocene (8–4 ka), and nine samples cover the late Holocene (4 ka to present).

Plant macrofossil assemblages

In total, 71 taxa were identified in the JTNP middens. Relative abundances of selected plant macrofossils through time are presented in Fig. 5(a) and (b) and the complete dataset can be accessed via the USGS/NOAA North American Packrat Midden Database, Version 3, 2006, <http://esp.cr.usgs.gov/data/midden/>. The two oldest assemblages are less diverse than those found later in the Pleistocene, but the very low diversity (seven species) in the >47 200 a BP midden may be due, at least in part, to the fact that this sample was very small and poorly preserved. Nevertheless, this midden contains *Pinus californiarum*, *Juniperus californica*, *Quercus cornelius-mulleri*, *Artemisia bigelovii/tridentata*-type (sagebrush), *Cercocarpus ledifolius* var. *intermontanus* (curl-leaf mountain mohogany) and *Purshia tridentata* var. *glandulosa* (antelope bush), species characteristic of Great Basin Conifer Woodland. The midden at 34 355 a BP likewise contains *Pinus californiarum*, *Juniperus californica* and *Quercus cornelius-mulleri*, but with a different assemblage of understory shrubs including *Brickellia*, *Ephedra*, *Ericameria cuneata* var. *spatulata*, *Peucephyllum schottii* and *Yucca* sp. All of these species except *Ephedra* are also found in the Late Pleistocene assemblages. Two middens from different locations (Hidden Valley and Jumbo Rocks) were dated at

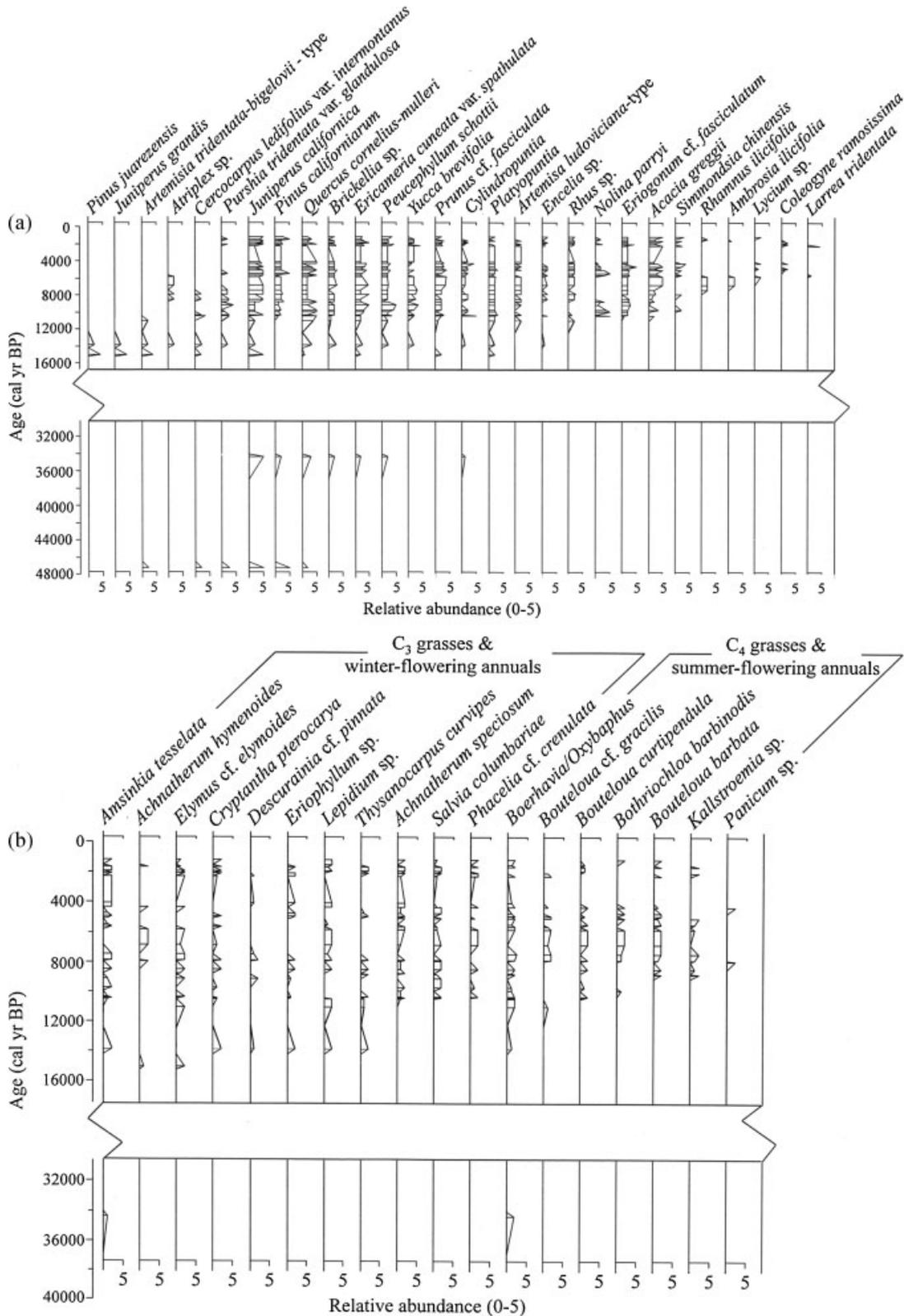


Figure 5 Plant macrofossil abundance through time for select species of trees, shrubs and cacti (a) and grasses and annuals (b)

14 990 and 13 880 a BP. Both of these middens contained *Pinus juarezensis*, *Juniperus grandis* and *Artemisia bigelovii/tridentata*-type, none of which grow at the site today. These middens also contained *Juniperus californica*, *Quercus cornelius-mulleri* and an understory of *Purshia tridentata* var. *glandulosa*, *Encelia*, *Ericameria cuneata* var. *spathulata*, *Peucephyllum schottii* and *Yucca brevifolia*. Ten Late Pleistocene–early Holocene samples dating from 11 055 to 8480 a BP document changes associated with the glacial–interglacial transition. This

period is marked by the disappearance of *Pinus juarezensis* and *Juniperus grandis* by 11 055 a BP, *Artemisia bigelovii/tridentata*-type by 10 470 a BP and the arrival of several new species including *Prunus fasciculata*, *Rhus*, *Acacia greggii* and the C₄ grasses *Bothriochloa barbinodis* (cane bluestem), *Bouteloua barbata* (six weeks grama), *Bouteloua curtipendula* (side-oats grama) and *Bouteloua cf. gracilis* (blue grama). During the middle Holocene (8–4 ka), *Cercocarpus ledifolius* var. *intermontanus* disappears and *Purshia tridentata*

var. *glandulosa* becomes rare in the midden assemblages. These more mesic shrubs are replaced by increasingly xeric-adapted species including *Ambrosia ilicifolia* (hollyleaf bursage), *Lycium*, *Simmondsia chinensis*, *Coleogyne ramosissima* and *Larrea tridentata*, indicative of a trend towards increased aridity.

Discussion

The midden series from JTNP indicates that the flora within the park has been surprisingly stable throughout the Late Pleistocene and Holocene. This stability appears to be the result of (1) the lack of extralocal species migrating into the area during the glacial period and (2) the early establishment and long persistence of many Mojave Desert elements in JTNP. On the other hand, C₄ grasses arrive at JTNP later than in the eastern Sonoran and northwestern Chihuahuan Deserts.

For the last glacial period, say from 40 to 13 ka, most midden series in the western USA are characterised by a number of extralocal species that today grow further upslope or to the north. With the exception of *Pinus juarensis* and *Juniperus occidentalis*, this was not the case at JTNP. The nearby San Bernardino Mountains support diverse forests containing *Abies concolor* (white fir), *Acer macrophyllum* (bigleaf maple), *Calocedrus decurrens* (incense cedar), *Cornus nuttallii* (Pacific dogwood), *Pinus coulteri* (Coulter pine), *Pinus jefferyi* (Jeffrey pine), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (ponderosa pine) and *Populus tremuloides* (quaking aspen), which reaches its southernmost distribution in the USA here. The lack of any of these species in middens from JTNP suggests that the late glacial midden series were probably too low (930–1357 m) to record downward displacement of trees and shrubs that characterise forests in the San Bernardino Mountains.

The lack of extralocal species does, however, allow us to place constraints on Late Pleistocene temperatures. Owen *et al.* (2003) studied laterofrontal moraines in the eastern San Bernardino Mountains and used equilibrium-line altitudes to reconstruct a July temperature reduction of 6.0–13.3°C from 16 to 12 ka BP. Owen *et al.* recognised that this estimate was inconsistent with packrat midden data, which suggests a temperature decrease of only about 6°C in the Mojave Desert (Spaulding, 1990). Our midden record, in closer proximity to the San Bernardino Mountains than other midden series, provides further evidence that the estimated decreases in LGM temperatures are too large. Assuming an environmental lapse rate of 6.5°C km⁻¹, a 6.5°C temperature depression would result in ~1000 m of downslope displacement of vegetation, and we would expect to find species now commonly growing around 2300 m in middens from the Late Pleistocene. We do not, however, find any evidence for these species (*Abies concolor*, *Pinus coulteri*, *Pinus jefferyi*, *Pinus lambertiana*, *Pinus ponderosa*) migrating into the area. Likewise, several species that are present in the middens during the Late Pleistocene, including *Ericameria cuneata* var. *cuneata*, *Peucephyllum schottii*, *Quercus cornelius-mulleri*, *Prunus fasciculata* and *Nolina parryi*, are not found at higher, colder elevations in the surrounding mountains today, suggesting temperatures could not have been as cold as the upper estimates suggested by equilibrium-line altitudes.

Two extralocal species that are found in the middens include *Pinus juarezensis* and *Juniperus grandis*. *Pinus juarezensis* and *Juniperus grandis* are found only in the middens dating to 14 990 and 13 880 a BP. As mentioned previously, the current

distribution of *Pinus juarezensis* extends from the San Jacinto Mountains south into Baja California, whereas *Juniperus grandis* occurs today in the San Bernardino Mountains to the northwest of JTNP (Miller *et al.*, 2005). Occurrence of these species in middens from near the end of the full glacial (14 990 a BP) and Bølling/Allerød (13 880 a BP), but not in middens from the earlier part of full glacial or Holocene, suggests that conditions during this time may have been somewhat cooler and/or wetter. In a recent study of hydraulic traits in junipers, Willson *et al.* (2008) found that *Juniperus californica* (collected from JTNP) was much more resistant to water stress than any of the other species measured, including *J. occidentalis*. It follows that more mesic conditions would have been necessary for less drought-resistant species like *Pinus juarezensis* and *Juniperus grandis* to move into JTNP during the late glacial.

On the other hand, the presence of *Pinus juarezensis* in JTNP during the Late Pleistocene represents a northward expansion of its range by ~50 km. The timing of its expansion corresponds to the end of the full glacial and Bølling/Allerød, which suggests that its more northerly presence may have been in response to warmer and drier climatic conditions. Northward surges in the ranges of *Pinus edulis* (Colorado pinyon) and *Pinus edulis* var. *fallax* (Arizona single-leaf pinyon) during the Bølling/Allerød have also been noted in the Sheep Range, NV, Wupatki National Monument, AZ, and in northeastern AZ (Kenneth L. Cole, pers. comm.).

In contrast to the range shifts seen in *Pinus juarezensis* and *Juniperus grandis* at JTNP, the regional boundary between *Juniperus californica* and *Juniperus osteosperma* during the Late Pleistocene appears to have been very similar to that of today. *Juniperus osteosperma* currently reaches the southern limit of its modern distribution on the northern piedmont of the San Bernardino Mountains just west-northwest of Yucca Valley. This species is absent from the JTNP midden record, which is dominated by *Juniperus californica*. This suggests that the boundary between these two species has been essentially unchanged for the past ~47 ka BP. On the other hand, *Juniperus californica* is found in midden records from the Kofa Mountains of Arizona (Van Devender, 1973), indicating expansion of its range to the southeast during the Pleistocene.

Also contributing to the relative stability of the flora is the early establishment and long-term persistence of many Mojave Desert elements in JTNP. Many of the species found in the full- to Lateglacial middens are still present at the site today, especially those species common to both the Mojave Desertscrub and Great Basin Conifer Woodland communities. Only a handful of mesic-adapted species disappeared during the glacial–interglacial transition (*Pinus juarezensis*, *Juniperus grandis*, *Artemisia bigelovii/tridentata*-type) or middle Holocene (*Cercocarpus ledifolius* var. *intermontanus* and *Purshia tridentata* var. *glandulosa*) as climate became more xeric. This stability may reflect wide ecological tolerances of the species and/or an elevation at JTNP that is near the lower/southern distribution limits for many species, such that movement of the species southward or downslope in response to more mesic Pleistocene climatic conditions did not produce the dramatic changes in species assemblages seen in many other midden records.

Yucca brevifolia is one of the species that arrives fairly early at 13 880 a BP and is stable throughout the Holocene within JTNP, although this can be contrasted with regional patterns and future predictions for its distribution. During the Pleistocene, *Yucca brevifolia* had a more expansive distribution, occurring in middens as far south as Organ Pipe National Monument (Van Devender, 1982), as far north as the Armagosa Desert and Sheep Range of southern Nevada (Spaulding, 1981, 1985) and as far east as the Waterman Mountains of southern

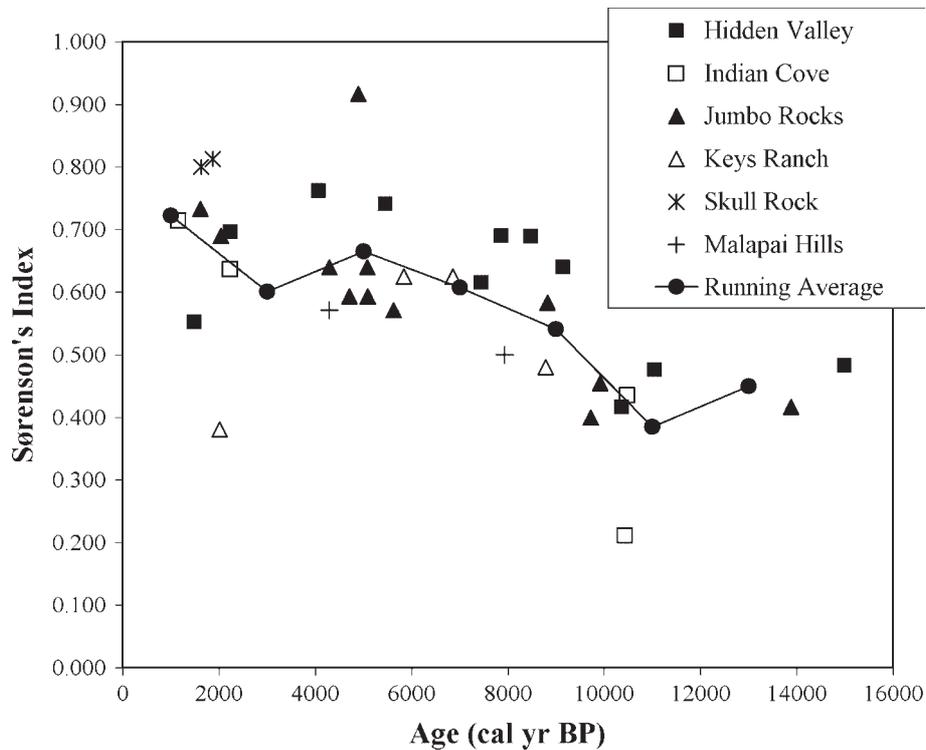


Figure 6 Sørensen's Similarity Index values calculated for the middens from JTNP and the modern vegetation at each midden collection site

Arizona (Anderson and Van Devender, 1991), whereas its subsequent Holocene history has been one of contraction from the southern and eastern limits of its Pleistocene range. Global warming may have a further, profound impact on the range of *Yucca brevifolia*. Cole *et al.* (2005) modelled the potential future climate space for *Yucca brevifolia* assuming $2\times$ the pre-industrial concentration of CO_2 . Their results indicate that the range for this species will likely be reduced and shifted northward by several hundred kilometres, requiring migration rates $10\times$ faster than its Holocene rate of $\sim 10 \text{ m a}^{-1}$ for many populations to remain viable; the persistence of *Yucca brevifolia* within JTNP at the current southern margin of its range is doubtful given this scenario.

Species typical of the Creosotebush Series of the Mojave Desertscrub/Sonoran Desert also arrived relatively early at JTNP. For example, *Simmondsia chinensis* appears in the JTNP midden series by 9720 a BP, but did not establish its easternmost outpost near the Arizona–New Mexico border until the last few centuries (Holmgren *et al.*, 2006). Physiography may be the key to explaining differences in the rates of postglacial migration of Sonoran Desert elements. The western and northern limits of many of these elements are set, rather abruptly, by the Transverse Ranges in southern California and the Mogollon Rim in central Arizona, respectively. Physiographic gradients are less abrupt along the transition from the Sonoran to Chihuahuan Deserts in southeastern Arizona. Accordingly, the northern and western limits of Sonoran Desert species were established relatively early in the Holocene, while species were slower to migrate to the east.

Sørensen's Similarity Index was used to quantify the stability of the vegetation assemblages observed in the midden record by providing a measure of the similarity between the fossil midden assemblages and the modern vegetation assemblage occurring within $\sim 100\text{m}$ of the midden sites. Sørensen's Similarity Index is expressed as $C = 2j / (a + b)$, where j = the number of species common to both assemblages, a is the total number of species in the first assemblage and b is the total number of species in the second assemblage (Cheetham and

Hazel, 1969; Magurran, 1988). Resultant values can range from 0.0 (assemblages completely dissimilar) to 1.0 (assemblages completely similar). To remove from consideration those species (e.g. annuals and biennials) with large year-to-year fluctuations in populations that may bias sampling due to their intermittent presence at a site, we restricted our assemblages to perennial trees, shrubs and succulents (Cole, 1985; Spaulding *et al.*, 1990).

Figure 6 shows Sørensen's Similarity Index values calculated for the middens from JTNP and the modern vegetation at each midden collection site. The overall trend in the data is an increase in similarity through time, although several patterns warrant discussion. First, two of the lowest similarity values occur during the full glacial period, as seen in the $>47\,000$ and $34\,355$ a BP middens (not shown on the graph). Notably, a value of 0 (no species in common) was found for the $>47\,000$ a BP midden, while the value for the $34\,355$ a BP midden was 0.21. Only six taxa could be identified in this small and partially decomposed midden, so small sample size likely contributed to the lack of similarity seen between the fossil and modern vegetation assemblages. Likewise, because similarity values for the full glacial are based on only two middens, more sampling will be needed to definitively assess whether the pattern seen is due to small sample size or actual dissimilarity in vegetation assemblages. Nevertheless, the pattern is consistent with the macrofossil assemblage data and it appears likely that vegetation assemblages during the full glacial were much less similar to the modern vegetation than those found from the Pleistocene–Holocene transition onward. By $\sim 10\text{ka}$ similarity values were on the rise and most sites show an overall increase in similarity values throughout the Holocene. For example, the average similarity value was only 0.368 for the period from 12 to 10 ka, rose to 0.541 for the period from 10 to 8 ka, was between 0.622 and 0.643 from 8 to 2 ka, and then rose again slightly to 0.722 during the period from 2 to 0 ka. Thus, by the end of the Pleistocene–Holocene transition, vegetation at JTNP contained many of the elements found there today and attests to the long-term stability of many species

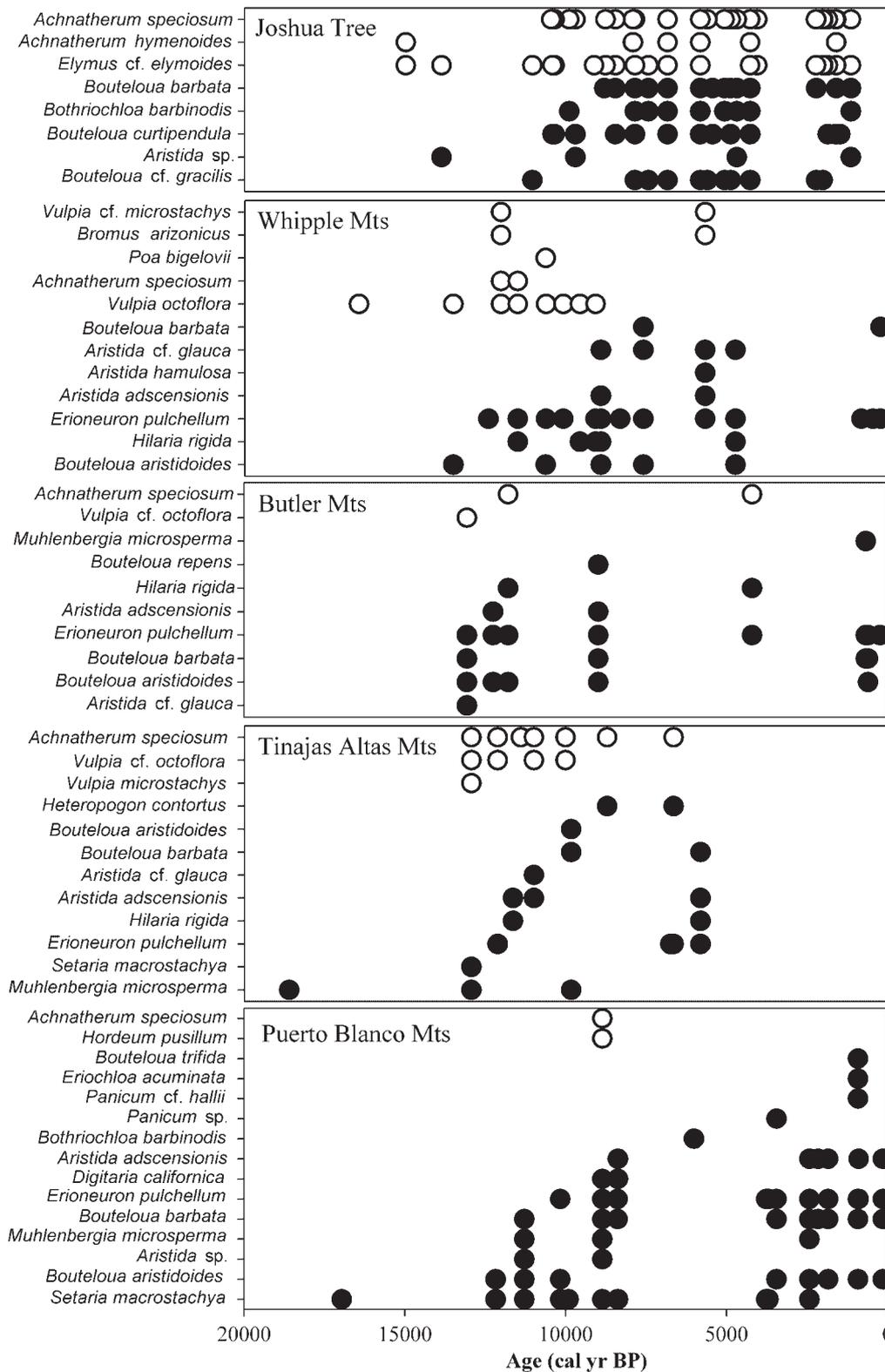


Figure 7 Records for C₃ grasses (open circles) vs. C₄ grasses (closed circles) from regional middens sites. Data for Puerto Blanco, Tinajas Altas, Butler, and Whipple Mountains from Van Devender *et al.* (1990)

throughout the Holocene. Thereafter, the arrival of more xeric-adapted species, especially during the mid to late Holocene (Fig. 5(a)), further increased similarity values.

Although Quaternary proxy records depicting relatively stable conditions do not typically garner as much attention as those that detail more dramatic environmental changes, these records still hold value for assessing current vegetation trends. Indeed, the recent historical changes at JTNP are all the more

remarkable given the overall stability seen throughout the Late Pleistocene and Holocene in the midden record. Over the past several decades, JTNP has experienced a dramatic increase in the abundance of invasive species, including *Brassica tournefortii* (Sahara mustard) and the annual grasses *Bromus* spp. and *Schismus* spp. These non-native grasses proliferate following wet years, leading to large fuel loads that serve to transmit fires in the Mojave Desert (Brooks and Matchett, 2006;

Brooks and Minnich, 2006). The impact of these invasive grasses in JTNP may be exacerbated by their ability to respond to increases in nitrogen from air pollution deposited downwind from the Los Angeles region (Allen *et al.*, 2007) and the prevalence of human-caused fires in low and middle elevations in the Mojave Desert as the population in the region grows (Brooks and Matchett, 2006). The midden record suggests that vegetation changes on the scale of those seen in the past few decades, or projected for the next few decades, were unprecedented during the Holocene.

Unlike the relatively early arrival of many Sonoran Desert species at JTNP, the arrival of C_4 grasses occurs later than in other records, suggesting a delayed arrival of monsoonal rainfall. Unlike C_3 grasses and winter and spring annuals, the presence of C_4 grasses and summer-flowering annuals is rare in the JTNP record prior to ~ 11 ka (Fig. 5(b)). Because these species respond to summer rainfall, this suggests little if any monsoon precipitation penetrated this far to the NW prior to the early Holocene. A comparison of the records for C_3 grasses vs. C_4 grasses (Fig. 7) from regional middens series indicates that C_4 grasses indicative of summer precipitation were present much earlier to the south and east of JTNP, allowing a rough delineation of the boundary for the northwestern extent of the North American Monsoon during the late Pleistocene. The arrival of summer precipitation and the associated suite of C_4 grasses and summer annuals in the early Holocene are consistent with the argument for greater summer insolation enhancing the magnitude and spatial extent of the monsoon during the early Holocene based on lake records from southern California (Bird and Kirby, 2006; Kirby *et al.*, 2007). Summer insolation at 30° N was highest between 13 and 9 ka, peaking at 11 ka (Berger and Loutre, 1991). The reason C_4 grasses and summer-flowering annuals remained rare prior to about 11 ka, even though insolation was relatively high by 13 ka, is unclear. It may be that insolation needed to reach a threshold level in order to initiate summer monsoonal rainfall and/or that vegetation exhibited a migrational lag following the advent of summer precipitation. Today, advection of monsoonal moisture further north or west than normal tracks the migration of the subtropical ridge to its northernmost position in southern Idaho, which in turn happens in summers when the polar jet is displaced farthest to the north in summer. At the very least, the absence of C_4 grasses in the midden series would suggest that the southerly displacement of the polar jet in summer blocked monsoonal moisture from reaching JTNP during the last glacial period.

Conclusions

This new packrat midden series from Joshua Tree National Park fills a spatial gap in midden coverage in the southwestern USA and provides a long-term record of vegetation change along the ecotone between the Sonoran and Mojave Deserts. One of the most notable trends in this record is the relative stability of many species within JTNP, including the park's namesake *Yucca brevifolia*. Factors contributing to this stability likely include the lack of invasion by extralocal species during the late glacial and the early establishment and persistence of many desert scrub elements. One exception to this is the arrival of C_4 grasses and summer-flowering annuals, consistent with the delayed onset of monsoonal precipitation, in the early Holocene. Although many species remain to be studied, modelled potential climate ranges for species such as *Yucca brevifolia* suggest a future for plant populations at JTNP that

stands in marked contrast to the past stability seen in the packrat midden record. Thus continued investigation of long-term patterns from packrat midden series to further refine the impact of climate change on vegetation, as well as the construction of modern and future bioclimatic envelopes for key species, will be critical for understanding the impacts of anthropogenic climate change on the unique vegetation of arid and semi-arid ecosystems of southwestern North America.

Acknowledgements We thank Nicholas Carlson, Dean Fujinami, Erin Gleason, Leslie Harper, Lorian Hornik, Angelica Longoria, Phyllis Nakagawa, Daniel Potts and Terri Wright for field and laboratory assistance. We also thank Paul DePrey, Gary Lindberg, Lora Lintz Mendoza, Alice Miller and Jason van Warmerdam for help with logistical arrangements and pinyon sample collection at Joshua Tree National Park, and Tasha La Doux for helpful discussions about oak taxonomy and identification. This manuscript was also improved through the constructive comments of Kenneth Cole and two anonymous reviewers. We thank John Southon and the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine, for assistance in obtaining radiocarbon dates. This project was funded by a Joshua Tree National Park Foundation Competitive Science Grant to CAH and a grant from Joshua Tree National Park through the University of Arizona's Desert Southwest Cooperative Ecosystem Studies Unit (DSCESU) to JLB. We thank Hank McCutchen of the National Park Service for approving the project and Larry Norris for delaying disbursement of DSCESU funds until JLB recuperated from a serious illness.

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