A 36,000-yr vegetation history from the Peloncillo Mountains, southeastern Arizona, USA

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Abstract

A 36,200 cal yr B.P. vegetation history was developed from macrofossils and pollen from 55 packrat middens from 1287 to 1442 m elevation in the Peloncillo Mountains of southeasternmost Arizona, USA. Today, these elevations are dominated by semidesert grassland with a mixture of Chihuahuan and Sonoran Desert shrubs, including an eastern disjunct population of jojoba (*Simmondsia chinensis*). From 36,200 to 15,410 cal yr B.P., rocky areas just above large, pluvial lakes that occupied what are now dry playas supported *Pinus edulis*, *Juniperus osteosperma*, *Juniperus* cf. *coahuilensis*, *Quercus* cf. *turbinella* and a rich understory of summer-flowering C_4 annuals and grasses, indicating abundant summer rains and mild winters. After ~15,410 cal yr B.P., *P. edulis* declined in abundance and disappeared briefly at 13,925 cal yr B.P., coincident with expansion of more xeric species and paleohydrological evidence for regional aridity during the Bølling–Allerød warm interval. *P. edulis* rebounded briefly during the Younger Dryas at 12,405 cal yr B.P. before disappearing along with other mesic woodland species sometime after 12,100 cal yr B.P. The few middens dating from the early to middle Holocene (10,000–4000 yr B.P.) indicate wetter conditions than today at 7790 cal yr B.P. followed by a general drying trend. The 35 middens from the late Holocene detail the sequential arrival of desertscrub species as vegetation became more modern in character.
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1. Introduction

In the American Southwest, there is a conspicuous gap in packrat midden coverage along the Continental Divide, specifically in the expansive semidesert grasslands that separate the northern reaches of the Chihuahuan and Sonoran Deserts just north of the USA/Mexico Border. Many species reach their eastern and western limits here despite it being the lowest place on the Continental Divide between Mexico and Canada, implying a climatic boundary rather than a physiographic barrier to dispersal. The region is characterized by ephemeral playas that held large pluvial lakes during the glacial period, and smaller, short-lived lakes in the Holocene (Long, 1966; Fleischhauer and Stone, 1982; Waters, 1989; Krider, 1998; Hawley et al., 2000; Castiglia and Fawcett, 2003). Questions remain about the timing and causes of lake level changes relative to other available paleoclimatic records such as vegetation histories from packrat middens.

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To bridge the midden gap, we developed a new packrat midden (*Neotoma* sp.) series from the Peloncillo Mountains Wilderness Area (PMWA) on the Arizona–New Mexico border (Fig. 1). The Peloncillo Mountains are ideally situated to address key biogeographic questions. The Apachian, Chihuahuan, Sonoran, and Southern Rocky Mountain–Mogollon floristic elements intersect here (McLaughlin, 1986, 1989), resulting in high levels of biodiversity. The Peloncillo midden record spans the last 36,200 cal yr at elevations near the highstands of nearby pluvial lakes (~1300–1500 m). We were able to reconstruct the lowest vegetation belt above pluvial lake shorelines as these highstands waxed and waned. Additionally, our reconstructions provide insight into past invasion and extinction dynamics of

several dominant species as their ranges adjusted to climatic changes.

2. Study area

The Peloncillo Mountains stretch northward from the Mexican border along the Arizona–New Mexico state line. Our study area is located within the PMWA, approximately 15 km northeast of San Simon, AZ, where the mountain range curves northwestward from New Mexico into Arizona. Here, the Peloncillo Mountains are flanked by the San Simon Valley to the west and the Animas Valley to the east. The area is part of the Mexican Highland section of the Basin and Range Physiographic Province, which is characterized by several
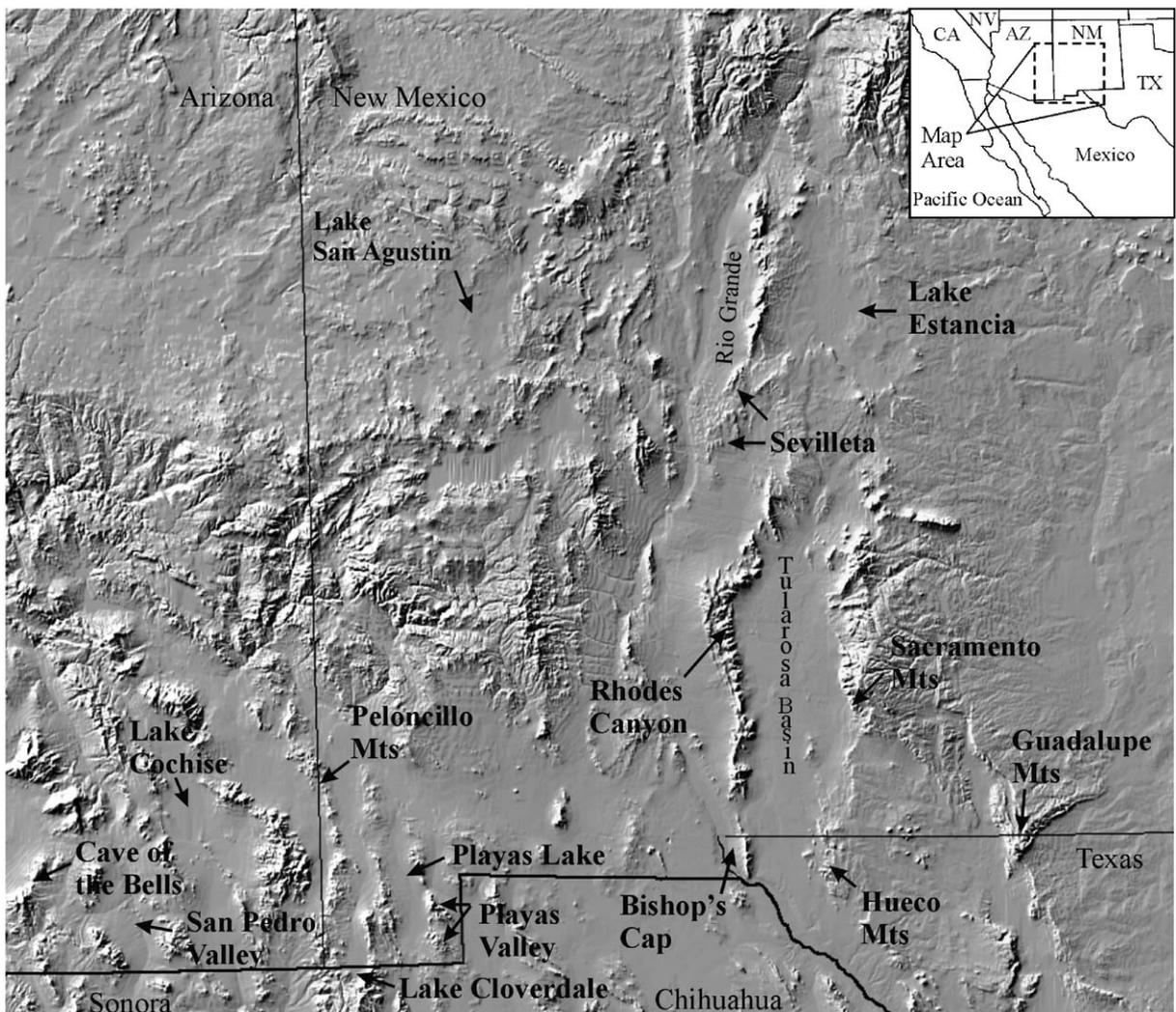

Fig. 1. Map of the study area showing the location of previous midden studies, the PMWA study site, pluvial lakes, and Paleoindian and megafauna sites.

northwest–southeast trending fault-block ranges separated by closed topographic basins. The PMWA consists primarily of massive Oligocene rhyolite flows and ash-fall tuff beds, and Oligocene and Eocene andesite and dacite flows. Coarse- to fine-grained Quaternary alluvium and fanglomerates comprise the lower pediments and alluvial fans (Drewes et al., 1985).

The average annual temperature at San Simon (1182 m) is 16.9 °C with monthly highs/lows averaging 35.8 °C/17.4 °C in summer (June–August) and 16.3 °C/−1.4 °C in winter (December–February). Annual precipitation averages 258.5 mm and exhibits a distinct seasonal cycle with an extremely arid foresummer (May–June), a summer precipitation maximum (July–August), and lesser and more variable amounts of precipitation in the remaining months of the year. The abrupt increase in San Simon and southwestern U.S. precipitation at the beginning of July coincides with development of a pronounced anticyclone at the jet stream level and a thermally-induced trough in the Chihuahuan and Sonoran Deserts, northward displacements of the Pacific and Bermuda highs, and the formation of southerly low-level jets over the Gulf of California. Prevailing winds shift from westerly to easterly as the monsoon anticyclone migrates to the north, and moisture is transported to the slopes of the Sierra Madre Occidental from the Gulf of California by southerly flow in the planetary boundary layer and from the Gulf of Mexico by southeasterly flow in the middle troposphere (for summary see Vera et al., in press). In its mature phase, the northern edge of the monsoon extends into Arizona and New Mexico subject to midlatitude effects. Monsoonal circulation and rainfall can persist into early September in southern Arizona, but retreat southward by late September with seasonal expansion of the midlatitude westerlies. Occasionally, low-pressure troughs or cutoff lows can steer moisture from dissipating tropical cyclones into Arizona over several days, producing record rainfall and flooding in the months of September and October. Precipitation in the cool months (November–April) is highly variable, depending on Pacific tropical sea surface temperatures and teleconnections with the subtropical jet and midlatitude westerlies.

In the PMWA, vegetation in the valleys and along the bajadas consists of *Larrea tridentata* with lesser amounts of *Prosopis glandulosa*, *Acacia constricta*, *Flournesia cernua*, and *Atriplex canescens* (Fig. 2). Hillslope vegetation is dominated by *L. tridentata*, *A. constricta*, *Parthenium incanum*, *F. cernua*, *Opuntia*, *Fouquieria splendens*, *Isocoma tenuisecta*, and *Pleuraphis* cf. *mutica*. Other hillslope vegetation includes a variety of shrubs and herbs (*Abutilon incanum*, *Acacia greggii*,

Fig. 2. Photograph looking NNE towards PMWA midden sites in West Doubtful Canyon. Vegetation along the bajadas and hillslopes is dominated by *Larrea tridentata*. Other common species are *Acacia constricta*, *Prosopis glandulosa*, *Flourensia cernua*, *Fouquieria splendens*, *Hilaria mutica*, and *Opuntia* spp.

Acourtia nana, *Asclepias linearis*, *Calliandra*, *Castilleja*, *Celtis pallida*, *Cryptantha*, *Dasylirion wheeleri*, *Daucus*, *Descurainia*, *Ephedra trifurca*, *Eriogonum*, *Gutierrezia sarothrae*, *Hibiscus*, *Lepidium*, *Nolina microcarpa*, *Plantago*, *Rhus microphylla*, *Senecio*, *Senna*, *Simmondsia chinensis*, *Sphaeralcea*, *Trixis californica*, and *Ziziphus obtusifolia*), cacti and succulents (*Cylindropuntia spinosior*, *Opuntia phaeacantha*-type, *Opuntia leptocaulis*, *Mammilllaria*, *Peniocereus greggii*, *Ferocactus wislizenii*, *Yucca baccata*, and *Yucca elata*), and grasses (*Aristida*, *Bothriochloa barbinodis*, *Bouteloua curtipendula*, and *Bouteloua gracilis*). *Juniperus* cf. *coahuilensis* and *Quercus* cf. *turbinella* are rare, but present at the higher elevations in our study area. Near our midden sites, *Celtis reticulata* and *Sapindus drummondii* are each represented by a single tree along a small mesic rock shelf with an intermittent spring. The presence of *S. chinensis* is notable because it represents an outlier population of this species, lying 40 km east of the nearest populations.

3. Methods

The nature of midden sampling has evolved over the last decade, at least within the U.S. Geological Survey–University of Arizona group based at the Desert Laboratory, allowing researchers to collect and analyze large numbers of middens. In the past, midden sampling usually involved two to three individuals collecting one or two dozen middens for a single chronology, the size of which was limited in part by available funds for radiocarbon dates. More recently, larger crews have been employed to comb the hillsides and generate series of >50 middens from a single site or elevation. Ready access to vacuum gas lines for pretreatment to CO_2 and graphite targets along with measurement discounts now make more extensive and well replicated midden chronologies possible.

Ninety-one middens were collected in caves and rock shelters from 1287 to 1485 m in the PMWA on the Arizona–New Mexico border (Fig. 3). Of these, 55 middens were selected for radiocarbon dating based on midden condition and composition. Middens were processed and analyzed according to well-established procedures (Spaulding et al., 1990). Midden material was screened through 2 mm (No. 10) and 1 mm (No. 18) sieves to separate size classes and facilitate sorting of plant remains. The 2-mm portion and a 1-g subsample from the 1-mm portion were sorted for plant macrofossils and used to assign relative abundances. All remaining material from the 1-mm fraction (16.0–168.2 g) was also examined for rare types. In addition, extracted bone,

insect, and charcoal remains provide a rich archive for future research. Macrofossil abundances were quantified using a relative abundance index of 0–5, where 0 = absent, 1 = single occurrence, 5 = dominant (Spaulding et al., 1990). The relative abundance index is a quick method for estimating variations in vegetation composition compared to absolute counts or pooled weights of individual species, which are ultimately subject to bias by midden size and dietary preferences of the rodents.

Small subsamples (∼20–30 g) of the indurated middens were removed for pollen analysis. Samples were rinsed in deionized water to remove pollen adhering to the surface and soaked in deionized water until disaggregated. The solution was stirred and a 50 ml aliquot of liquid collected. The liquid was treated with hot 10% KOH to remove humic acids followed by hot water washes. Next, 10% HCl and *Lycopodium* tracers were added. This was followed by HF treatment to eliminate silicates, concentrated HCl to remove carbonates, acetolysis, and a second KOH and hot water wash. The residue was mounted in glycerine and each sample counted beyond a sum of 300 terrestrial grains. After 300 grains, the slide was scanned for poorly represented types. In the case of several of our samples, this procedure resulted in pollen slides too sparse to count, so the above process was repeated using 100 ml of liquid. We used Tilia 2.0 and Tiliagraph (Grimm, 1991–1993) to plot macrofossil abundances and pollen percentages and a constrained incremental sum of squares (CONISS) cluster analysis (Grimm, 1987) to group the assemblages based on similarity of flora.

Radiocarbon determinations were performed using between 3 and 7 mg of material from individual plant species. All samples 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. Dates are reported as the midpoint of calibrated radiocarbon age ranges; radiocarbon dates and calibrated age ranges can be found in Table 1. The Calib 5.0.1 Intcal04 calibration curve was used for samples <21,000 ^{14}C yr B.P. (Stuiver and Reimer, 1993) and the CalPal CalPal2004_SFCP curve used for samples >20,000 ^{14}C yr B.P. (www.calpal.de).

4. Results

4.1. Radiocarbon dating

Radiocarbon dates for the Peloncillo Mountains middens range from 36,200 to 140 cal yr B.P. (Table 1).

Seventeen middens date from the Pleistocene, including three from the Younger Dryas period (12,900–11,600 cal yr B.P.). Three middens date from the middle Holocene (8000–4000 cal yr B.P.) and 35 from the late Holocene (<4000 cal yr B.P.). In the case of WDC-15C, temporal mixing was suspected based on traces of *P. glandulosa* and *D. wheeleri* in association with what appeared to be a glacial-aged vegetation assemblage. This was confirmed by an AMS date of 21,170 cal yr B.P. from *Pinus edulis* needles, while *P. glandulosa* dated to 6625 cal yr B.P. Based on floral composition, we believe 21,170 cal yr B.P. is an accurate date for most of the assemblage and the *P. glandulosa* and *D. wheeleri* are younger contaminants. There was insufficient material for AMS dating to determine whether traces of *P. edulis* in another midden dated at 5750 cal yr B.P. represent mixing or long-distance transport by birds.

4.2. Plant macrofossil assemblages

Relative abundances of selected plant macrofossils through time are summarized in Fig. 4. In total, 113 taxa were identified from the middens. The complete data set can be accessed online (http://esp.cr.usgs.gov/data/midden). Vegetation from the Last Glacial Maximum (LGM) through 20,875 cal yr B.P. was dominated by *P. edulis* and *Juniperus osteosperma*. *J. osteosperma* possesses unusual sunken stomates that were also seen in two late glacial middens from the nearby Playas Valley (Holmgren et al., 2003), but were not identified correctly until the present study. *J.* cf. *coahuilensis* identification was based on its somewhat flattened leaves and visible stomates located above the intersection of the overlying leaf or scale (Betancourt et al., 2001). *J.* cf. *coahuilensis* is rare in LGM middens, but becomes more common by
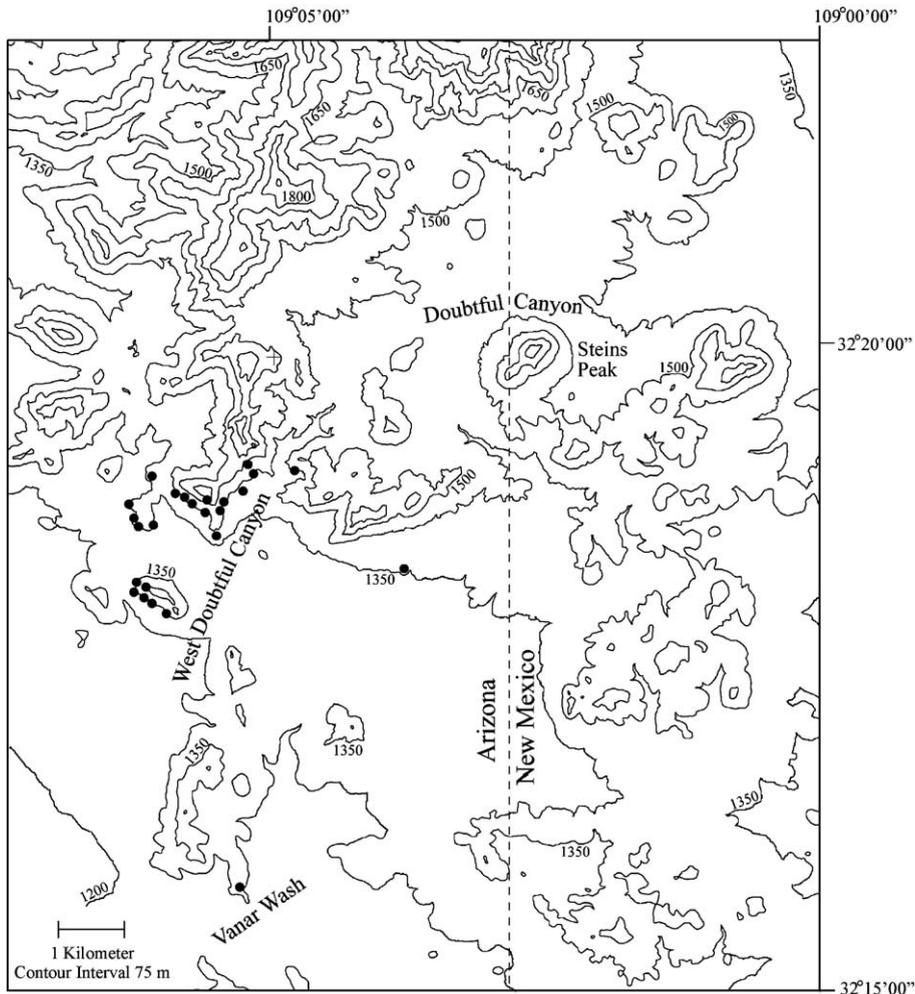

Fig. 3. Topographic map with location of middens from the PMWA.

Table 1
Site locations and radiocarbon dates for the PMWA packrat middens

Midden designation	Latitude (°S)	Longitude (°W)	Elevation (m)	Slope aspect	^{14}C age (yr B.P.)	S.D.	$d^{13}C$ (‰)	Lab code	Calibrated (2s) age range (yr B.P.)	Midpoint	# of taxa identified
Doubtful Canyon Camp 91B	32° 18.972	109° 04.889	1390	S	150	30	−10.7	AA58752	0–283	140	44
W. Doubtful Canyon 4B	32° 18.737	109° 05.430	1398	E	170	30	−24.4	AA55761	0–290	145	36
W. Doubtful Canyon 16	32° 18.647	109° 05.602	1395	S	180	50	−22.2	AA56001	0–300	150	29
W. Doubtful Canyon 4A	32° 18.737	109° 05.430	1398	E	395	30	−20.3	AA55760	322–511	470	28
W. Doubtful Canyon 37B	32° 18.731	109° 05.548	1431	ESE	925	30	−23.2	AA58750	773–924	850	40
W. Doubtful Canyon 9B	32° 18.609	109° 05.789	1402	S	1130	30	−23.5	AA58758	962–1167	1065	26
W. Doubtful Canyon 9D	32° 18.609	109° 05.789	1402	S	1140	35	−20.9	AA54660	966–1170	1070	35
W. Doubtful Canyon 66A	32° 17.943	109° 05.909	1343	SE	1194	35	−22.5	AA55762	1001–1255	1130	34
W. Doubtful Canyon 38C	32° 18.753	109° 05.528	1421	E	1265	40	−20.8	AA54663	1082–1285	1180	40
W. Doubtful Canyon 40A	32° 18.791	109° 05.541	1430	E	1280	50	−22	AA5598	1080–1290	1185	43
W. Doubtful Canyon 40C	32° 18.791	109° 05.541	1430	E	1310	35	−22.9	AA55757	1178–1294	1235	41
W. Doubtful Canyon 14B	32° 18.801	109° 05.553	1435	E	1485	35	−21.6	AA55747	1302–1507	1405	41
W. Doubtful Canyon 14C	32° 18.801	109° 05.553	1435	E	1485	35	−22.9	AA55764	1302–1507	1405	46
W. Doubtful Canyon 14A	32° 18.801	109° 05.553	1435	E	1495	40	−23.2	AA55763	1304–1515	1410	40
W. Doubtful Canyon 38A	32° 18.753	109° 05.528	1421	E	1555	45	−22.4	AA55996	1352–1535	1445	43
W. Doubtful Canyon 34B	32° 18.742	109° 06.336	1366	SW	1685	40	−22.2	AA54665	1520–1704	1610	32
W. Doubtful Canyon 38D	32° 18.753	109° 05.528	1421	E	1825	50	−22.4	AA54661	1620–1880	1750	40
W. Doubtful Canyon 10B	32° 18.004	109° 06.558	1439	S	2060	45	−21.9	AA54659	1903–2143	2025	29
W. Doubtful Canyon 34C	32° 18.742	109° 06.336	1366	SW	2070	40	−20.9	AA54664	1933–2144	2040	41
W. Doubtful Canyon 32G	32° 18.673	109° 06.206	1333	ESE	2075	45	−22.9	AA55994	1925–2152	2040	44
W. Doubtful Canyon 10A	32° 18.004	109° 06.558	1439	S	2100	70	−22.4	AA56002	1900–2310	2105	32
W. Doubtful Canyon 57C	32° 18.985	109° 06.171	1370	W	2165	30	−24.8	AA58760	2061–2309	2185	37
W. Doubtful Canyon 34A	32° 18.742	109° 06.336	1366	SW	2185	30	−21.5	AA58749	2121–2312	2215	28
W. Doubtful Canyon 38B	32° 18.753	109° 05.528	1421	E	2235	45	−22.2	AA55995	2149–2341	2245	38
W. Doubtful Canyon 57B	32° 18.985	109° 06.171	1370	W	2395	35	−21.8	AA55755	2159–2356	2260	39
W. Doubtful Canyon 32F	32° 18.673	109° 06.206	1333	ESE	2405	35	−20.7	AA55759	2345–2696	2520	39
Vanar Wash Cave 17D	32° 15.772	109° 05.352	1267	SE	2,429	41	−23.5	AA54666	2351–2702	2530	24

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W. Doubtful Canyon 9A	32° 18.609	109° 05.789	1402	S	2530	40	−20.1	AA55749	2473–2747	2610	37
W. Doubtful Canyon 42	32° 18.203	109° 06.363	1321	SSW	2530	70	−23	AA56000	2360–2750	2555	43
W. Doubtful Canyon 9C	32° 18.609	109° 05.789	1402	S	2540	50	−24.5	AA55997	2380–2760	2570	40
W. Doubtful Canyon 32D	32° 18.673	109° 06.206	1333	ESE	2925	40	−23	AA54580	2958–3211	3085	31
W. Doubtful Canyon 15G	32° 18.754	109° 05.639	1442	S	2985	40	−22.7	AA54577	3006–3328	3170	37
Doubtful Canyon Camp 91A	32° 18.972	109° 04.889	1390	S	3020	35	−21.5	AA58751	3080–3341	3210	32
W. Doubtful Canyon 32A	32° 18.673	109° 06.206	1333	ESE	3100	40	−23.5	AA58748	3215–3395	3305	37
W. Doubtful Canyon 32E	32° 18.673	109° 06.206	1333	ESE	3485	50	−19.9	AA55999	3640–3880	3760	37
W. Doubtful Canyon 43	32° 18.790	109° 06.352	1287	W	4750	40	−22	AA55756	5327–5588	5460	39
W. Doubtful Canyon 15H	32° 18.754	109° 05.639	1442	S	4990	45	−22.3	AA54579	5608–5891	5750	31
W. Doubtful Canyon 57D	32° 18.985	109° 06.171	1370	W	6925	55	−23.7	AA54662	7660–7920	7790	36
W. Doubtful Canyon 23B	32° 18.949	109° 05.833	1485	S	10315	55	−21.8	AA54581	11,830–12,390	12110	28
W. Doubtful Canyon 15E	32° 18.754	109° 05.639	1442	S	10320	55	−23.1	AA54571	11,840–12,390	12115	26
W. Doubtful Canyon 20B	32° 18.983	109° 05.982	1417	S	10465	55	−21.2	AA54578	12,150–12,660	12405	30
Doubtful Canyon Camp 91C	32° 18.972	109° 04.889	1390	S	11230	55	−22.6	AA58753	12,990–13,240	13115	28
W. Doubtful Canyon 57E	32° 18.985	109° 06.171	1370	W	11635	55	−19.9	AA54582	13,340–13,650	13495	33
W. Doubtful Canyon 23A	32° 18.949	109° 05.833	1485	S	12075	55	−20.6	AA54585	13,790–14,060	13925	30
W. Doubtful Canyon 15F	32° 18.754	109° 05.639	1442	S	12740	55	−18.5	AA54575	14,780–15,280	15030	31
W. Doubtful Canyon 32C	32° 18.673	109° 06.206	1333	ESE	13025	55	−21.6	AA54570	15,100–15,720	15410	38
W. Doubtful Canyon 32B	32° 18.673	109° 06.206	1333	ESE	13160	55	−22.2	AA54574	15,240–15,930	15585	31
W. Doubtful Canyon 24A	32° 18.698	109° 06.232	1364	WSW	14050	55	−21.5	AA54583	16,350–17,100	16725	22
W. Doubtful Canyon 24B	32° 18.698	109° 06.232	1364	WSW	14160	55	−20.4	AA54667	16,470–17,280	16875	29
W. Doubtful Canyon 57A	32° 18.985	109° 06.171	1370	W	17670	55	−19.2	AA54584	20,550–21,200	20875	22
W. Doubtful Canyon 15C	32° 18.754	109° 05.639	1442	S	17930	55	−19.3	AA58746	20,840–21,500	21170	31
W. Doubtful Canyon 15C	32° 18.754	109° 05.639	1442	S	5838	41	−21.4	AA58747	6505–6746	6625	Prosopis
W. Doubtful Canyon 31	32° 18.136	109° 06.217	1343	S	18590	55	−18.1	AA54573	22,050–22,330	22190	15
W. Doubtful Canyon 15B	32° 18.754	109° 05.639	1442	S	25260	220	−22.7	AA58759	29,670–30,790	30230	17
W. Doubtful Canyon 15D	32° 18.754	109° 05.639	1442	S	27180	280	−22.8	AA54572	30,920–32,320	31620	18
W. Doubtful Canyon 32H	32° 18.673	109° 06.206	1333	ESE	31090	450	−17.3	AA55758	35,300–37,110	36205	29
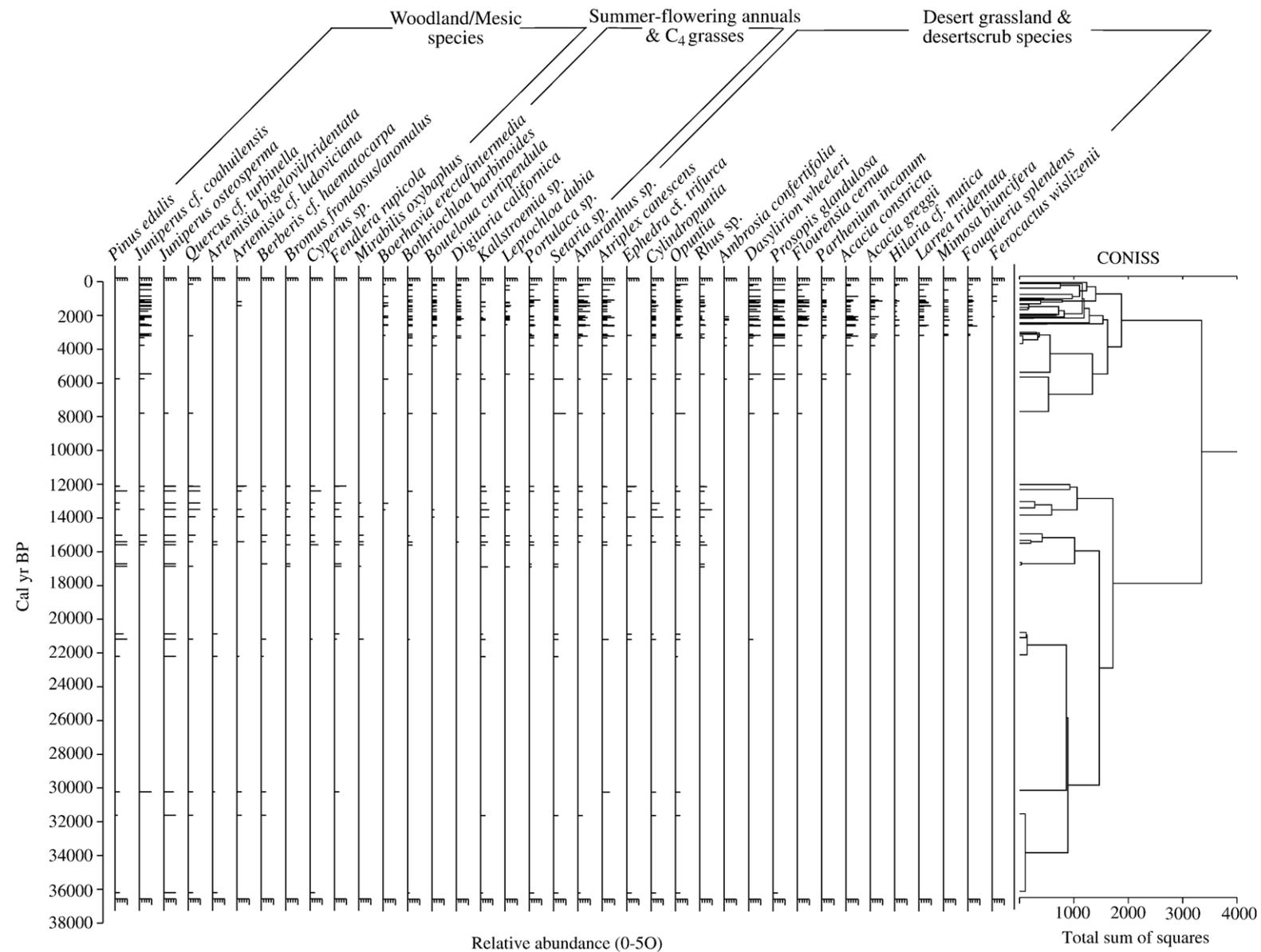
Fig. 4. Plant macrofossil abundance through time for select species from PMWA and CONISS cluster analysis.
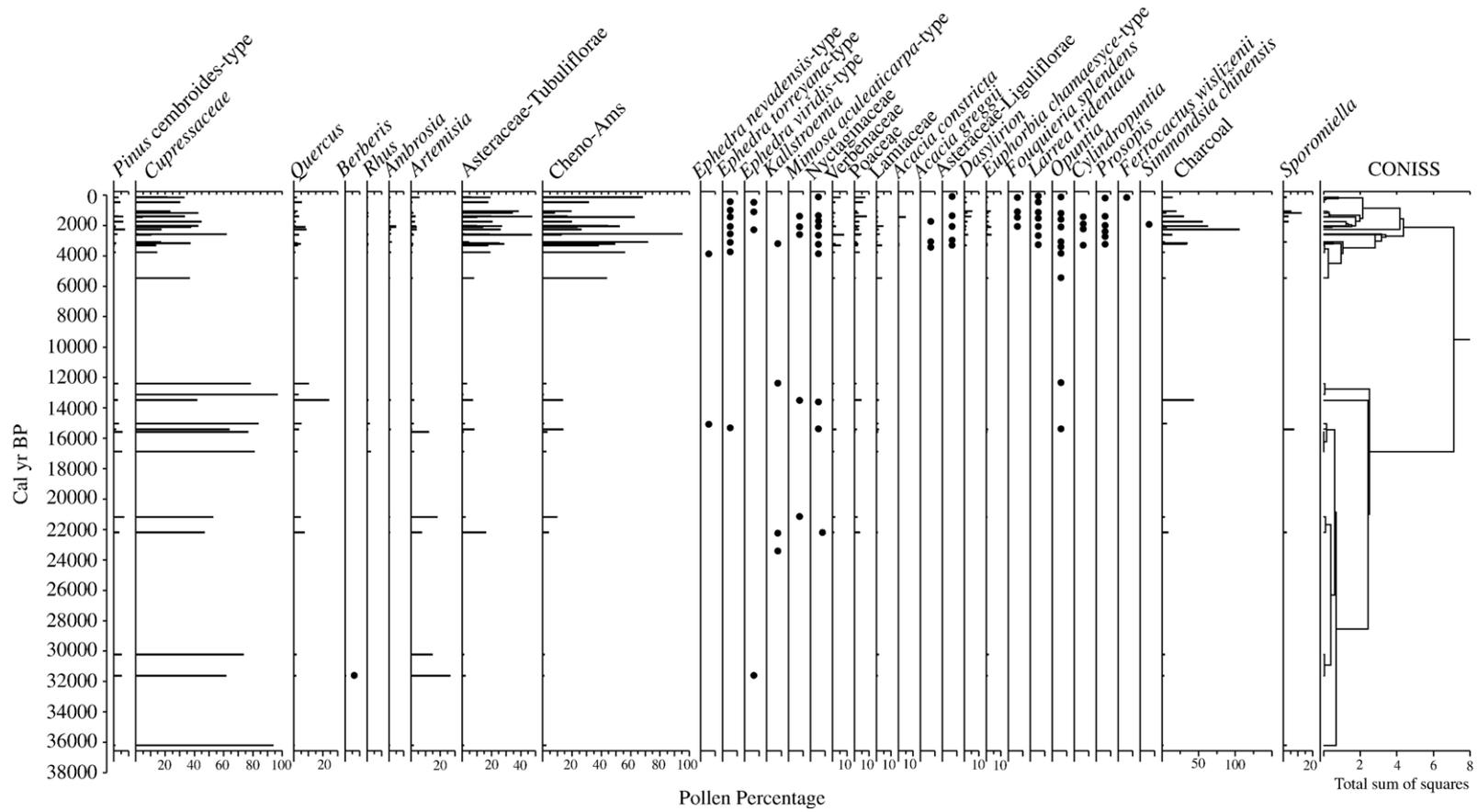
Fig. 5. Pollen percentages through time for select species from PMWA and CONISS cluster analysis. Filled circles indicate pollen percentages <3%.
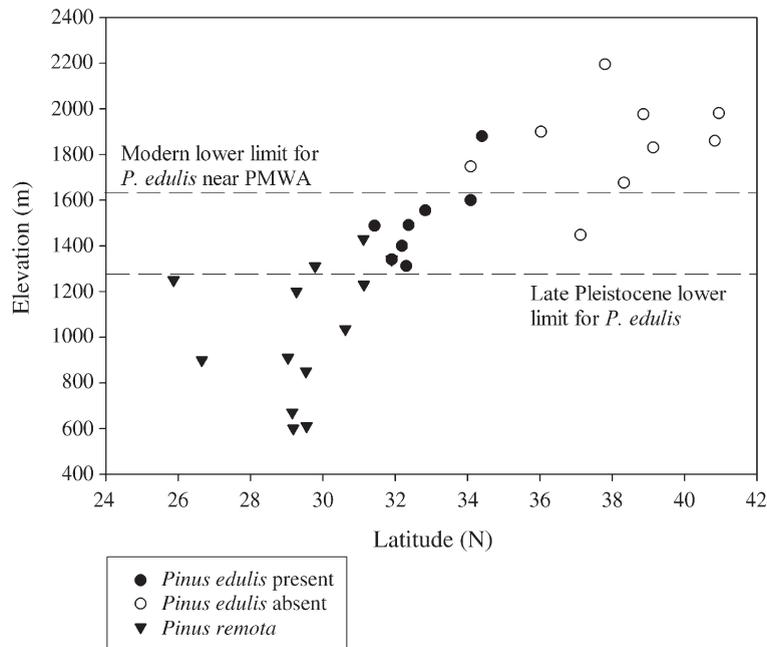
Fig. 6. Latitudinal and elevational distribution of glacial-age pinyon pines in the northern Chihuahuan Desert.

16,875 cal yr B.P. *Q.* cf. *turbinella*, *Artemisia bigelovii/tridentata*, *Berberis* cf. *haematocarpa*, *Cyperus*, *Fendlera rupicola*, and *Mirabilis oxybaphoides* are all found throughout the Pleistocene, but are rare or absent in the Holocene.

Several species are present in both Pleistocene and Holocene middens including several summer-flowering annuals and C_4 grasses. These species include *Boerhavia erecta/intermedia*, *Bothriochloa barbinoides*, *B. curtipendula*, *Digitaria californica*, *Kallstroemia*, *Leptochloa dubia*, *Portulaca* and *Setaria*. Other persistent species include those with cosmopolitan distributions such as *A. canescens*, *E. trifurca*, *Opuntia* spp., and *Rhus*. The wide ecological tolerances of these plants allow them to occur in communities ranging from woodlands to desertscrub.

After ~15,410 cal yr B.P. *P. edulis* declines in abundance and disappears briefly at 13,925 cal yr B.P. Significantly, the disappearance of *P. edulis* occurs in a midden from the site with the highest elevation (WDC-23A, 1485 m). This suggests *P. edulis* had retreated upslope by this time, possibly due to a decrease in effective moisture. Concurrently, an expansion is seen in the more xeric species *Q.* cf. *turbinella*, *Opuntia* spp., *E. trifurca*, and *Rhus*. The change in vegetation at this time is apparent in the cluster analysis, which indicates that assemblages prior to 15,030 cal yr B.P. are more similar to LGM assemblages than to those from 13,925 cal yr B.P. onward. *P. edulis* rebounded by 12,400 cal yr B.P. before

disappearing along with other mesic Pleistocene species sometime after 12,110 cal yr B.P.

Only three middens date between 8000 and 4000 cal yr B.P. The midden at 7790 cal yr B.P. contains a mix of mesic species (*J. osteosperma*, and *Q.* cf. *turbinella*), summer-flowering annuals and C_4 grasses, and the first desert grassland/desertscrub species (*D. wheeleri*, *P. glandulosa*, and *F. cernua*). By 5460 cal yr B.P. all of the mesic species had disappeared and were replaced by the characteristic Chihuahuan Desert elements *P. incanum* (by 5750 cal yr B.P.) and *A. constricta* (5460 cal yr B.P.). Although these assemblages contain a mix of mesic and xeric species, cluster analysis indicates they are more similar to late Holocene assemblages than late Pleistocene ones. The subsequent arrival of increasingly xeric species into the area is detailed by the 35 middens from the late Holocene. *L. tridentata* first arrives at 3170 cal yr B.P., *F. splendens* by 2570 cal yr B.P. and *F. wislizenii* by 2040 cal yr B.P.

4.3. Pollen assemblages

At total of 67 different pollen types were identified in our record and common types are summarized in Fig. 5. Due to the small size of the midden, we were unable to set aside a separate indurated piece for pollen analysis in the 7790 cal yr B.P. midden. During the Pleistocene, the pollen record is dominated by Cupressaceae (41.4–96.4%) with *Artemisia* subdominant (up to 26%).

Cupressaceae pollen almost certainly represents *Juniperus*, since this is the only genus present in the macrofossil record. We cannot rule out *Cupressus arizonica*, however, which occurs commonly today along canyon streams. Other common late glacial pollen types include *Quercus*, *Pinus*, Asteraceae, Chenopodiaceae–Amaranthaceae, Poaceae, and *Rhus*. The decline in *P. edulis* and increase in xeric species from ~15,410 to 13,115 cal yr B.P. seen in the macrofossil record are mirrored by changes in pollen percentages. Although never abundant in the entire midden record (<10%), *Pinus* pollen decreases from 15,410 to 12,405 cal yr B.P., while *Quercus*, Asteraceae–Tubuliflorae, and Chenopodiaceae–Amaranthaceae pollen percentages increase. Cluster analysis also indicates a change in vegetation assemblages between 15,030 and 13,495 cal yr B.P. During the Holocene, *Artemisia*, Cupressaceae, and *Quercus* percentages decline, while Chenopodiaceae–Amaranthaceae, Asteraceae, and charcoal increase dramatically. Chenopodiaceae–Amaranthaceae and Asteraceae–Tubuliflorae pollen reach percentages up to 94.9% and 47.4%, respectively, during the late Holocene. Small amounts of the dung fungus *Sporomiella* are seen throughout the record and most likely reflect animal activity in caves and rock shelters in the PMWA.

5. Discussion

5.1. Pollen–macrofossil comparison

The pollen record enabled us to glean information on regional vegetation including the species that most likely populated the valleys in the PMWA. Macrofossils provide a taxonomically detailed record of species growing within ~50 m of den sites, but are biased towards rocky hillsides and provide little information about vegetation growing on lower alluvial fans and valley floors or in the surrounding mountains. Pollen, on the other hand, can be incorporated into middens via packrat pellets and feces, by adhering to local plants collected by the rodents, or by airborne transport from both local and more distant sources (Davis and Anderson, 1987). Overall, the pollen and macrofossil records from the PMWA are remarkably similar, with a few notable exceptions. *Pinus* pollen percentages are lower than expected based on macrofossil abundance, although the underrepresentation of *Pinus* pollen in middens compared to macrofossils (Thompson, 1985) and the modern pollen rain (Martin, 1963; Anderson and Van Devender, 1991) has been demonstrated previously. On the other hand, *Artemisia* is much more abundant in the pollen record during the late glacial period than indicated by macrofossils, suggesting that

although it was uncommon along the hillslopes, it may have dominated along the lower bajadas and in the valleys. The pollen record also indicates both *Ambrosia* and Lamiaceae were more common than their rare occurrences in the macrofossil record suggests.

5.2. Pleistocene biogeography and climate

During the late Pleistocene, increased effective moisture filled now-dry playa basins and dramatically changed the character of the surrounding vegetation. The PMWA midden record indicates pinyon–juniper woodland with scattered oaks expanded downslope to ~1300 m along pluvial lake margins into what is now Chihuahuan desertscrub. These woodlands were dominated by *P. edulis* and *J. osteosperma* with smaller amounts of *J.* cf. *coahuilensis* and *Q.* cf. *turbinella.* The understory consisted of mesic C_3 woodland species and summer-flowering annuals and C_4 grasses.

Middens from the PMWA further refine the Pleistocene biogeography of *P. edulis*. Although *P. edulis* is the dominant species today in the northern Chihuahuan Desert, it was restricted to southern New Mexico, southeastern Arizona, and far west Texas during the Pleistocene (Lanner and Van Devender, 1981, 1998). Combined with other midden records from the Chihuahuan Desert, our evidence suggests that glacial-age *P. edulis* occurred between ~1300 and 1700 m at 31–34° N (Fig. 6). The presence of *P. edulis* at 1333 m in the PMWA represents a displacement downslope of at least ~250 m and is similar to its lower limit seen in other late Pleistocene records from the region. *P. edulis* descended to 1488 m in the Playas Valley of New Mexico on xeric limestone substrate (Holmgren et al., 2003), to 1400 m at Bishop's Cap, NM, and to 1340 m in the Hueco Mountains of west Texas (Van Devender and Spaulding, 1979). At lower elevations to the south in the Chihuahuan Desert, *P. edulis* is replaced by *Pinus remota*, which was more widely distributed during the late Pleistocene (Lanner and Van Devender, 1981, 1998). In the Hueco Mountains, remains of both *P. edulis* and *P. remota* have been identified from glacial-age middens, possibly defining a hybrid zone (Van Devender, 1990).

Estimates of Pleistocene temperatures and precipitation can be gleaned from the climatic tolerances of C_4 grasses and *P. edulis*. C_4 grass distribution is correlated with relatively high temperatures and precipitation, particularly during the summer growing season (Paruelo and Lauenroth, 1996; Epstein et al., 1997; Yang et al., 1998). The lower limits of *P. edulis*, on the other hand, are apparently controlled by high soil surface temperatures and soil moisture deficit (Linton et al., 1998; Williams and

Ehleringer, 2000). *P. edulis* is capable of exploiting summer monsoonal precipitation from soil moisture in shallow surface layers, but its roots become inactive at high soil temperatures (Williams and Ehleringer, 2000). *P. edulis* is also susceptible to xylem cavitation during periods of summer moisture stress (Linton et al., 1998). Given that *P. edulis* requires a minimum of ~120–135 mm of annual precipitation (Burns and Honkala, 1990; Thompson et al., 1999), much less than the present value of 259 mm for the PMWA, heat load and associated moisture stress appear to be the most likely factors restricting its distribution at this location. We can thus infer from the fact that C_4 grasses co-occur with *P. edulis* in glacial-age middens that late Pleistocene climates in the PMWA must have been cool enough to allow *P. edulis* to expand downslope, but not so cold as to exclude C_4 grasses.

Historical climatic data from the range margins of four C_4 grasses found in glacial-aged middens (*B. barbinodis*, *D. californica*, *L. dubia*, and *Setaria macrostachya*) allows us to determine climatic tolerances for these species. Minimum growing season temperatures today at the northern margins for these species are up to 5.9 °C lower than in the PMWA, while winter temperatures are up to 5.7 °C lower. Minimum summer (JJA) precipitation is 49 mm, or ~50% of the modern value of 105 mm in the PMWA. This indicates a 5.7–5.9 °C reduction in temperatures and up to 50% reduction in summer precipitation in the PMWA during the late glacial could still support a C_4 grass understory.

P. edulis no longer occurs in the PMWA, but White Signal, NM (1850 m), located 72 km to the northeast in pinyon–juniper woodland in the Burro Mountains, provides a suitable analog for late glacial climates. Mean annual precipitation at White Signal is 381 mm (an increase of 122 mm), mean annual temperature 12.4 °C (a decrease of 4.5 °C), and mean summer temperature 22.8 °C (a decrease of 4.7 °C). A temperature decrease of 4.5–4.7 °C and a 47% increase in precipitation during the late glacial encompass the tolerances of the C_4 grasses and are consistent with lake budget estimates for Paleolake Estancia ~345 km to the northeast in New Mexico (Leopold, 1951; Menking et al., 2004).

Although Pleistocene middens from other Chihuahuan Desert sites contained C_4 grasses (Van Devender and Riskind, 1979; Van Devender et al., 1984; Van Devender, 1990; Van Devender, 1995), the PMWA series is notable for its diversity and abundance of summer-flowering annuals and C_4 grasses. The PMWA record includes the mid-summer annuals *Kallstroemia*, *Boerhavia*, and *Portulaca*, and the C_4 grasses *B. barbinodis*, *Bouteloua* cf. *gracilis*, *D. californica*, *L.*

dubia and *Setaria* cf. *macrostachya*. Middens from the Playas Valley just to the southeast (Holmgren et al., 2003) include *Kallstroemia*, *Boerhavia*, *B.* cf. *gracilis*, *B. barbinodis*, *D. californica*, *Muhlenbergia* sp., and *Setaria* sp. The late glacial importance of C_4 grassland in the region was inferred previously from vertebrate remains (Harris, 1987), from carbon isotope values from soil carbonates (Liu et al., 1996; Monger et al., 1998; Buck and Monger, 1999), and from megaherbivore tooth enamel (Connin et al., 1998). Our records from the PMWA and Playas Valley provide direct evidence for the presence of a wide suite of C_4 species in the Arizona–New Mexico border region.

Taken at face value, the presence of summer-flowering annuals and C_4 grasses within woodland midden assemblages from the PMWA, together with carbon isotopic evidence for their regional importance in soil carbonates (Cole and Monger, 1994; Liu et al., 1996; Monger et al., 1998) and megaherbivore tooth enamel (Connin et al., 1998; Koch et al., 2004), would seem to indicate relatively warm temperatures and abundant summer precipitation. C_4 grasses, characteristic of modern desert grasslands in the Southwest, utilize shallow surface moisture during the summer growing season (Neilson, 1986; Archer, 1994). Growing season temperature has long been recognized as a primary control on C_4 plant distribution and recent work has also demonstrated the positive correlation of C_4 grass distribution with mean annual precipitation and proportion of summer precipitation (Paruelo and Lauenroth, 1996; Epstein et al., 1997; Yang et al., 1998). The paleoclimatic interpretation for relatively wet glacial summers may not be straightforward, however. For example, some of the C_4 grasses in the midden record (*Botriochola barbinoids*, *D. californica*, and *S. macrostachya*) are opportunistic and may respond to available moisture regardless of season (Van Devender et al., 1990). This argument, however, seems less likely to apply to the entire suite of C_4 grasses and summer-flowering annuals identified from Pleistocene middens. Additionally, several authors have suggested the lower atmospheric pCO_2 levels during the glacial period could have shifted the competitive edge from C_3 to C_4 species (Cole and Monger, 1994; Connin et al., 1998; Koch et al., 2004). If lower CO_2 played such a prominent role, however, C_4 grasslands should have been more prevalent globally than indicated by the fossil record.

The prevalence of C_4 annuals and grasses in addition to C_3 trees and shrubs in the northern Chihuahuan Desert indicates biseasonal moisture similar to the modern regime. The expansion of pinyon–juniper woodland and C_3 understory shrubs is a clear response to increased

winter rainfall, whereas the rich understory of summer-flowering C_4 annuals and grasses also indicates abundant summer rains. Furthermore, the virtual absence of C_4 annuals and grasses in late Pleistocene middens from the southern Colorado Plateau and points north (Betancourt, 1984, 1990) suggests that the northern monsoon boundary was perhaps more well defined and abrupt than today. The simplest explanation is that the North American Monsoon as modulated by the Sierra Madre Occidental was relatively intact in the glacial period, but stronger midlatitude effects truncated the northern fringes of the monsoon. These midlatitude effects probably included a more persistent snowpack in the Rockies and Colorado Plateau and southward displacement of the westerlies in summer, which would have suppressed formation of a thermally induced trough and limited the northward migration of the monsoon anticyclone over the Four Corners region.

Whatever the explanation, the northern Chihuahuan Desert may have been one of the few areas in the western half of the coterminous United States to "green-up" in July and August during the late Pleistocene. The mid-summer green-up may have provided forage and seasonal refuge from the dry fire season (July–October) at higher latitudes, and may explain the concentration of megafaunal and Paleoindian sites in the area (Haury et al., 1953, 1959; Haynes, 1991).

5.3. Pleistocene–Holocene transition

The decline in *P. edulis* from 15,410 to 13,115 cal yr B.P. in the Peloncillo Mountains is coincident with other regional records of aridity during the Bølling–Allerød warm period (Fig. 7). *P. edulis* exhibits a similar decline in abundance between 14,800 to 13,900 cal yr B.P. in midden records from the Hueco Mountains of western Texas (Van Devender and Riskind, 1979; Van Devender, 1990), while both *P. edulis* and *Juniperus scopulorum* decline from 15,270 to 13,670 cal yr B.P. in Rough Canyon, New Mexico (Betancourt et al., 2001). Nearby pluvial Lake Cochise desiccated following highstands prior to 16,670 cal yr B.P. and from 16,400 to 15,925 cal yr B.P. (Waters, 1989). In the San Pedro Valley deposition of the Coro Marl, a spring-fed marsh deposit, ceased ∼15,600 yr B.P. as groundwater levels began to decline (Haynes, 1987, 1991; Pigati et al., 2004).
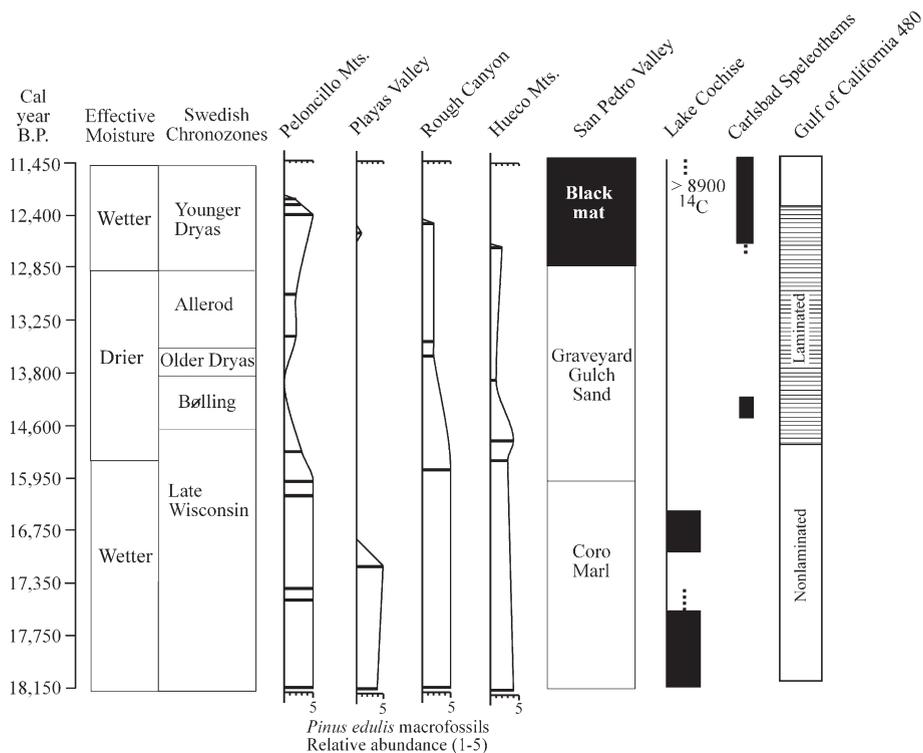

Fig. 7. Diagram of records showing changes in effective moisture during the Late Pleistocene–Holocene transition. Data is based on: Playas Valley (Holmgren et al., 2003), Rough Canyon (Betancourt et al., 2001), Huecos Mountains (Van Devender and Riskind, 1979); San Pedro Valley (Haynes, 1991; Pigati et al., 2004); Lake Cochise (Waters, 1989); Carlsbad Canyon (Polyak et al., 2004); and Gulf of California (Keigwin and Jones, 1990). Black areas indicate wetland deposits(San Pedro Valley), lake highstands (Lake Cochise), and speleothem growth (Carlsbad).

Groundwater reached its lowest level during the "Clovis-aged Drought" just before 12,750 cal yr B.P., coincident with extinction of the Rancholabrean megafauna (Haynes, 1991). Late Pleistocene drying is also noted in Lakes Estancia (Allen and Anderson, 2000) and San Agustin (Markgraf et al., 1984; Phillips et al., 1992) to the northeast, suggesting a regional-scale hydrologic response. In the Guadalupe Mountains of New Mexico, a hiatus in stalagmite growth likewise indicates drying during the Bølling–Allerød (Polyak et al., 2004), while a high-resolution oxygen isotope record in speleothems from Cave of the Bells in the Santa Rita Mountains southeast of Tucson, AZ also indicates warmer/drier conditions (Wagner et al., 2003).

After 13,115 cal yr B.P., *P. edulis* abundance increases dramatically to 12,405 cal yr B.P. during the Younger Dryas period. Because the rebound in *P. edulis* is documented in only one midden, it may be premature to attribute it to a Younger Dryas climate reversal until the pattern can be replicated. Unfortunately this pattern is not replicated in other midden records because the last occurrences of *P. edulis* are slightly earlier in these records and sampling densities are low. Regional paleohydrologic records, however, do provide evidence for a return to wetter conditions during the Younger Dryas. In the San Pedro Valley the water table rebounded by 12,830 cal yr B.P. and began depositing black organic mats, which have been AMS dated to the Younger Dryas (Haynes, 1991; Jull et al., 1998). Stalagmite growth in the Guadalupe Mountains reinitiated soon after the start of the Younger Dryas, although it is notable that growth continued for a millennium after the termination of the Younger Dryas (Polyak et al., 2004). A Younger Dryas return to cooler/wetter conditions is also found in oxygen isotopic trends in carbonate from Cave of the Bells (Wagner et al., 2003).

A notable similarity exists between terrestrial records from the southwestern United States and oceanic records from the northeast Pacific Ocean. Bølling, Allerød, and Younger Dryas climate events are recorded in foraminiferal faunal assemblages, oxygen isotope values, and changes in lamination preservation in cores from the Gulf of California (Keigwin and Jones, 1990) and Santa Barbara Basin (Kennett and Ingram, 1995; Behl and Kennett, 1996; Cannariato et al., 1999; Hendy and Kennett, 1999). This linkage is not unexpected given that the northeast Pacific is a major source of moisture for the southwestern United States and suggests a common climatic forcing. Several possible climatic mechanisms controlling conditions in the northeast Pacific and southwestern United States have been invoked. Based on the apparent synchroneity between abrupt changes in the Santa Barbara Basin and Greenland temperatures, Hendy et al. (2002) proposed an atmospheric linkage between the North Atlantic and North Pacific with warming in both areas related to contraction of the Polar gyre. In the North Pacific, an associated contraction of the Aleutian Low and northward migration of the North Pacific High should have resulted in a weakened California Current, warmer sea surface temperatures (SST), and a more northerly jet stream, consistent with warmer temperatures and decreased moisture in the southwestern United States. The similarity of high-resolution oxygen isotope results from Cave of the Bells with Greenland ice core records likewise supports a coupling between the North Atlantic and the North Pacific (Wagner et al., 2003). Alternatively, Clement et al. (2001) suggest abrupt events such as the Younger Dryas may result from orbitally driven changes in the tropical Pacific that cause ENSO to lock to the seasonal cycle for several centuries, producing La Niña-like conditions. However, modern teleconnections between ENSO and the southwestern United States typically result in drier conditions during La Niña events, making persistent La Niña-like SST changes during the Younger Dryas inconsistent with the cooler/wetter conditions seen in paleoclimate records. On the other hand, if La Niña-like SSTs affected the North Atlantic thermohaline circulation (Schmittner et al., 2000), associated changes in the North Pacific may have trumped other teleconnections to the southwestern United States.

5.4. The middle Holocene

The middle Holocene (8000–4000 cal yr B.P.) period is represented by only three middens in our series. These indicate wetter-than-present conditions at the beginning of this period followed by a general drying trend. The scarcity of middens from the middle Holocene, a common pattern across the southwestern United States (Webb and Betancourt, 1990), has been variously attributed to both increased moisture and increased aridity. Preservation of packrat middens is affected by the hygroscopic nature of the crystallized urine matrix (amberat). Amberat forms a rind around middens and protects contents from microbial and chemical decay and insect attack (Spaulding et al., 1990). During humid periods, amberat may fail to crystallize or may rehydrate and flow, eventually leading to midden destruction. This explanation seems unlikely, however, given that middens are common in our record from the wetter late Pleistocene. On the other hand, prolonged winter drought could lead to a decline in woody perennials that respond primarily to winter moisture, and a subsequent decrease in packrat populations and midden

production (Spaulding, 1991; Betancourt et al., 1993). Yet another possibility is that prolonged drought could have increased foraging range, increased susceptibility to predators, and thus shortened longevity. Because packrats tend to be solitary and tend to occupy a single den, shortened longevity could significantly affect midden formation.

Comparison of midden and paleohydrological evidence reveals discrepancies for the middle Holocene. Beach ridge and lacustrine deposits from Laguna El Fresnal and Laguna Santa María, 70 km south of the U.S.–Mexico border, record evidence for highstands from 7585 to 6980 and 4795 to 4220 cal yr B.P., which have been attributed to greater winter storm frequency (Castiglia and Fawcett, 2003). The earlier highstand corresponds to the more mesic conditions seen in the midden at 7790 cal yr B.P., while the highstand from 4795 to 4220 cal yr B.P. may correspond to a rise in Lake Cochise that occurred ∼4500–3080 cal yr B.P. Notably, this later fluctuation seen in pluvial lakes is not apparent in the vegetation record. This could be due to the discontinuous nature of the midden record and the relatively small number of middens dating to this period. It may also be that lakes are more sensitive to precipitation variability than vegetation. Changes in vegetation composition are subject to migrational lags, and may or may not respond to a series of exceptionally wet or dry years. On the other hand, playas in the southwestern United States have been observed to fill after large rainstorms. Thus, lakes may fill and desiccate

much more quickly and record changes that occur on decadal or shorter timescales.

5.5. Late Holocene

The late Holocene is marked by the progressive arrivals of more xeric species as Chihuahuan and Sonoran Desertscrub elements migrated into the area. For example, *A. constricta* appeared by 5460 cal yr B.P., *L. tridentata* by 3170 cal yr B.P., *F. splendens* by 2750 cal yr B.P. and *F. wislizenii* by 2040 cal yr B.P. The record of *F. wislizenii* in the PMWA is the first documented occurrence of this species in middens from the Chihuahuan Desert. *F. wislizenii* was present much earlier in the Silverbell (14,290 cal yr B.P.; Lanner and Van Devender, 1974; Van Devender and Spaulding, 1979) and Puerto Blanco Mountains (12,180 cal yr B.P.; Van Devender, 1987) of the Sonoran Desert in southern Arizona. Its slow migration into the PMWA may be due to rare establishment events and the extremely slow growth rate of seedlings (Shreve, 1917).

The arrival time of *S. chinensis* is less clear. The local, disjunct population of *S. chinensis* is the easternmost documented population of this species, suggesting that the local population in the PMWA arose from long-distance dispersal from populations to the west (Fig. 8). *S. chinensis* macrofossils are absent from all middens, and it is indicated by only two pollen grains in the 2260 cal yr B.P. midden. The trace amount of pollen could signal either the first occurrence of the species in the regional
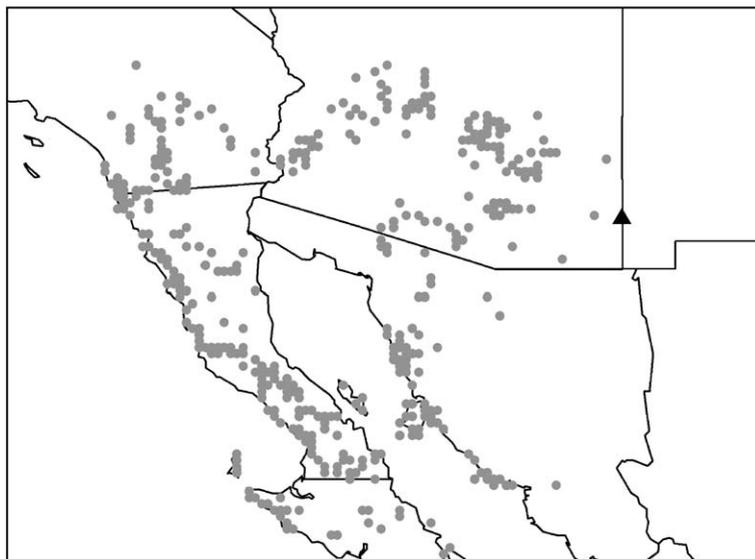

Fig. 8. Distribution of *Simmondsia chinensis* populations in the southwestern United States. The disjunct population at the PMWA is indicated by the large black triangle.

record or it may be due to contamination by modern pollen. Unfortunately, we cannot radiocarbon date the pollen and it thus confounds interpretation. Typically, after the first appearance of a species in the pollen record its presence becomes common in subsequent younger samples. *S. chinensis* pollen is not seen in any younger middens, suggesting that the occurrence in the 2260 cal yr B.P. may be due to modern contamination. This would suggest that the population of *S. chinensis* in the PMWA may have become established only within the last few centuries. If so, it would appear that the ranges of some Sonoran desertscrub elements may still be expanding into this area. Alternatively, if *S. chinensis* did arrive by 2260 cal yr B.P., this disjunct population has remained localized rather continuing its eastward expansion or backfilling to the west.

6. Conclusions

A new middens series from the Peloncillo Mountains in southeastern Arizona bridges geographical coverage in midden records in the Southwestern United States and allows for the reconstruction of paleoenvironments during the late Pleistocene and Holocene. Increased moisture during the late Pleistocene resulted in filling of playa basins and the expansion of pinyon–juniper woodlands and C_3 woody shrubs downslope. The presence of summer-flowering annuals and C_4 vegetation in the understory indicates summer precipitation and relatively warm conditions during the late glacial, suggesting that desert grassland species and the core area of the Mexican–Southwestern U.S. monsoon remained more or less intact from glacial to interglacial periods. During the Bølling–Allerød, *P. edulis* declines and vegetation becomes more xeric, similar to the patterns of aridity seen in other regional records. During the Younger Dryas, *P. edulis* rebounds, coincident with the return to mesic conditions noted elsewhere in the Southwest. Unfortunately, little information can be gleaned about the early and middle Holocene periods due to the scarcity of middens dating to this period. In the late Holocene, the arrival of Chihuahuan Desertscrub species signals the transition to increasingly xeric conditions. The disjunct population of *S. chinensis* at the eastern extreme of its range may indicate continued adjustment of species ranges in the broad transitional area between the Sonoran and Chihuahuan Deserts.

Acknowledgements

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