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A vegetation history from the arid prepuna of northern Chile (22–23°S) over the last 13 500 years

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Abstract

The Quaternary paleoclimate of the central Andes is poorly understood due to numerous discrepancies among the diverse proxy records that span this geographically and climatically complex region. The exact timing, duration and magnitude of wet and dry phases are seldom duplicated from one proxy type to another, and there have been few opportunities to compare climatic records from the same proxy along environmental gradients. Vegetation histories from fossil rodent middens provide one such opportunity on the Pacific slope of the Andes. We previously reported a vegetation history from the upper margin (2400–3000 m) of the absolute desert in the central Atacama Desert of northern Chile. That record identified a distinct wet phase that peaked between 11.8 and 10.5 ka, when steppe grasses and other upland elements expanded as much as 1000 m downslope, and a secondary wet period during the middle to late Holocene (7.1–3.5 ka). The latter wet phase remains controversial and is not as readily apparent in our low-elevation midden record. We thus sought to replicate both phases in a midden record from the mid-elevations (3100–3300 m) of the arid prepuna, where slight precipitation increases would be amplified. Midden records from these elevations identify conditions wetter than today at 13.5–9.6, 7.6–6.3, 4.4–3.2 and possibly 1.8–1.2 ka. Dry phases occurred at 9.4–8.4 ka and possibly at ca. 5.1 ka. Present floras and modern hyperarid conditions were established after 3.2 ka. The records from the two elevational bands generally match with some important differences. These differences could reflect both the discontinuous aspect of the midden record and the episodic nature of precipitation and plant establishment in this hyperarid desert.

Keywords: rodent middens; vegetation history; Holocene; prepuna; Atacama Desert; northern Chile; central Andes

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1. Introduction

Discrepancies in timing, magnitude and direction of climate change are common among diverse paleoclimate records in the central Andes. These inconsistencies may be due to poor dating, varying temporal resolution, different response times and sensitivities to both temperature and precipitation, disagreements about field evidence and climatic interpretation, or simply the sheer vastness and geographic complexity of the region across which we are trying to find correlation. Because much of the research is recent and many of the proxies are unique, few records have yet been replicated. Multiple cores can usually be taken and compared from a single site, but there is only one Nevado Sajama (Thompson et al., 1998) and only one Lake Titicaca (Seltzer et al., 1998; Baker et al., 2001b). Syntheses of central Andes paleoclimatology to some extent involve comparing apples and oranges with few chances to duplicate the same kind of record at multiple localities. During the past 3 years, we have been developing vegetation and groundwater histories from fossil rodent middens and wetland deposits, respectively, along a 1500-km transect on the Pacific slope of the central Andes (Betancourt et al., 2000; Holmgren et al., 2001; Placzek et al., 2001; Rech et al., 2001; Latorre et al., 2002; Rech et al., 2002). A strength of this paleoclimate transect is the ability to apply the same methodologies across broad elevational, latitudinal, climatic, vegetation and hydrological gradients.

Here we present a 13 500-year vegetation history gleaned from plant macrofossil analysis of 44 rodent middens collected in the upper part (3100–3300 m) of the 'prepuna' vegetation belt (as defined in Villagrán et al., 1983) along the Pacific slope of the Andes within the central Atacama Desert. In a previous study, we focused on rodent middens in the transition from prepuna to absolute desert between 2400 and 3000 m (Betancourt et al., 2000; Latorre et al., 2002). The prepuna is a sparsely vegetated zone, with individual plants every few meters to tens of meters, that grades into absolute desert at lower elevations (< 2400 m) and into low (< 1 m tall) shrublands of the 'tolar' zone at higher elevations (> 3400 m).

Among the major findings from our earlier study was that, between 16.2 and 10.5 ka, indicator species from both tolar (3400–4000 m) and Andean steppe (4000–4800 m) expanded downslope 400–1000 m across the edge of absolute desert, where precipitation is now insufficient to support vascular plants. The period appeared to be wettest between 11.8 and 10.5 ka. We estimated that the vegetation expansions required a three- to five-fold increase in summer precipitation (30–50 mm today vs. 100–150 mm during the pluvial period). These late glacial–early Holocene middens contain C_4 annuals and perennials that flower in summer, indicating that precipitation was augmented by greater 'spillover' of western Altiplano convective storms onto the Pacific slope of the Andes. In the central Atacama, both lake (Grosjean, 1994; Bobst et al., 2001; Grosjean et al., 2001) and groundwater levels (Betancourt et al., 2000; Rech et al., 2002, 2003) were at their highest during the late glacial–early Holocene (~ 16–9 ka).

We also found rodent midden assemblages slightly wetter than today between 7.1 and 3.5 ka, in agreement with rising groundwater levels inferred from wetland deposits (Rech et al., 2002, 2003). At these lower elevations, the mid-Holocene precipitation increase was much less than the increase during the late glacial–early Holocene, and was thus harder to quantify from the rodent midden record. Currently, there is considerable debate over whether the middle Holocene was wet (Quade et al., 2001) or dry (Grosjean, 2001) in the central Atacama. At stake is the precipitation history of the central Atacama Desert, which does not appear to be linked to variations in seasonal insolation over the central Andes, but rather to sea surface temperature gradients in the tropical Pacific and associated upper air circulation anomalies over the western Altiplano.

In order to replicate the late glacial–early Holocene pluvial and better evaluate mid-Holocene climate, we have developed midden series from multiple localities in the upper part of the prepuna (3100–3300 m), located 50–300 m higher in altitude and some 100 km north of our low-elevation sites in the central Atacama. The slightly higher densities of perennial plants and midden-forming rodents (*Lagidium*, *Phyllotis*, *Abrocoma*) at these middle elevations ensure an abundant Holocene midden record. Changes in precipitation and temperature should have different effects on the midden record. Increases/decreases in precipitation should increase/decrease species richness by way of the enrichment of the prepuna belt with species from higher vegetation belts. More importantly, precipitation increases of only 10–50% over modern values could have displaced tolar and steppe species downslope into the upper prepuna, amplifying precipitation signals that were barely registered in the prepuna–absolute desert transition. On the other hand, lower temperatures reduce species richness due to lower productivity, with the added possibility of bringing down some of cold ‘specialists’ typical of the uppermost vegetation belts, such as cushion and rosette plants.

2. Physical setting

2.1. Physiography

The hyperarid Atacama Desert extends along the Pacific Andean slope from the southern border of Peru (18°S) to Copiapó, Chile (27°S) (Rundel et al., 1991). This study focuses on the central part of the Atacama (22–24°S) near the Tropic of Capricorn and centered on a conspicuous, structural embayment along the Andean front. Two major mountain ranges, the Cordillera Domeyko and the Cordillera de los Andes, run from north to south across our study area, partially enclosing the Calama (or Río Loa) Basin and completely enclosing the Salar de Atacama Basin (Fig. 1). The main Andean front consists of late Tertiary and Quaternary ignimbrites and volcanic rocks, with both extinct and active volcanoes forming the highest peaks between 5000 and 6000 m. The Chilean Altiplano above 4000 m is dotted with large salars (salt basins) and a few small lakes (e.g. Laguna Lejía and Miscanti); salars occupy large expanses along the base of the Andes below 2500 m. Branching off the western Andean slope at 22°15′S, the Cordillera Domeyko spans approximately 4° in latitude and runs parallel to the main Andean front. Here, this range includes late Paleozoic and Cretaceous folded sedimentary rocks partially overlain by Oligo–Miocene alluvial fanglomerates, occasionally capped by erosional remnants of late Miocene ignimbrites (Marinovic and Lahsen, 1984). In this sector, most of the Cordillera Domeyko lies at 3000–3500 m, with a maximum altitude of 4278 m at Cerro Quimal.

2.2. Climate

Aridity in the Atacama region may have begun as early as the Eocene and evolved into hyperaridity by the middle Miocene (Alpers and Brimhall, 1988; Mortimer, 1980; Stoertz and Ericksen, 1974). The hyperaridity is due to the extreme rainshadow of the high Andes, which blocks the advection of tropical/subtropical moisture from the southern Amazon Basin; the blocking influence of the semi-permanent South Pacific Anticyclone, which limits the influence of winter storm tracks from the south; and the generation of a temperature inversion at ∼1000 m by the cold and north-flowing Humboldt Current, which limits inland (upslope) penetration of Pacific moisture (Borgel, 1973; Caviedes, 1973).

The scant annual precipitation that falls in the Atacama consists of fog and occasional winter rains in all coastal areas below 1000 m, occasional winter (May–October) rains on Andean slopes south of 25°S, and summertime (November–March) storms that cross the Altiplano, spill over the Andes, and rain out on the Pacific slope north of 25°S. In the monsoonal part of the Atacama (18–25°S), absolute precipitation amounts depend on elevation and distance from the crest of the Andes, which control the rainout from convective storms as air masses descend down the Pacific slope. The hyperarid core of the Atacama, where rainfall is currently insufficient to support vascular plants, spans an elevational range of 3500–1000 m in the most arid sector (24–26°S), tapering gradually to the north and abruptly to the south. In the central Atacama, estimated mean annual rainfall averages 0–20 mm at 1000–

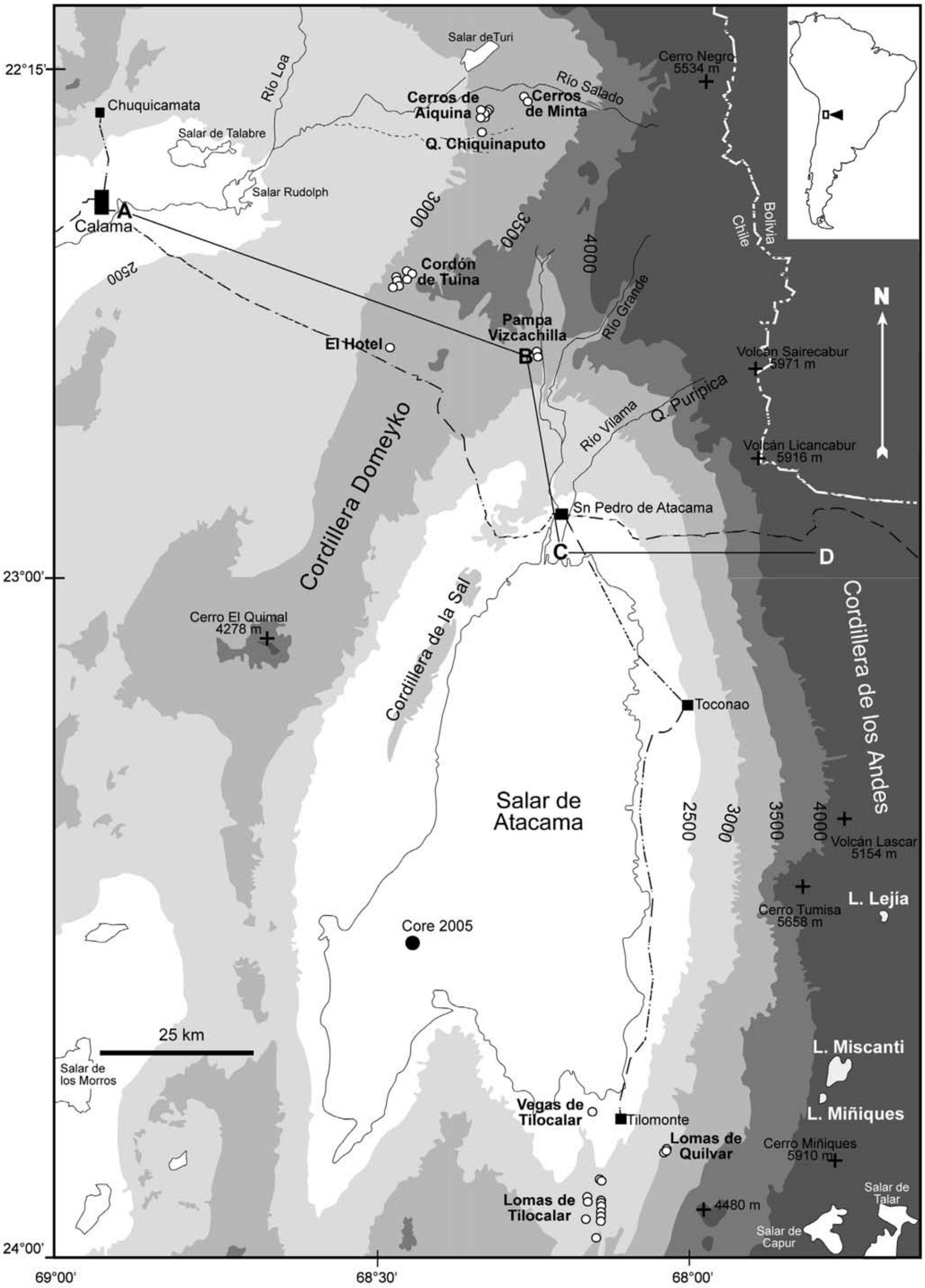

Fig. 1. Map of the central Atacama Desert indicating location of midden sites discussed in this study and those from the southern tip of the Salar de Atacama published in Latorre et al. (2002). Other key paleoclimate sites also shown include core 2005 (Bobst et al., 2001), Laguna Lejía (Grosjean, 1994; Geyh et al., 1999), Laguna Miscanti (Grosjean et al., 2001) and Quebrada Puripica (Grosjean et al., 1997a). Letters ABCD denote the altitudinal transect discussed in Figs. 2 and 3.

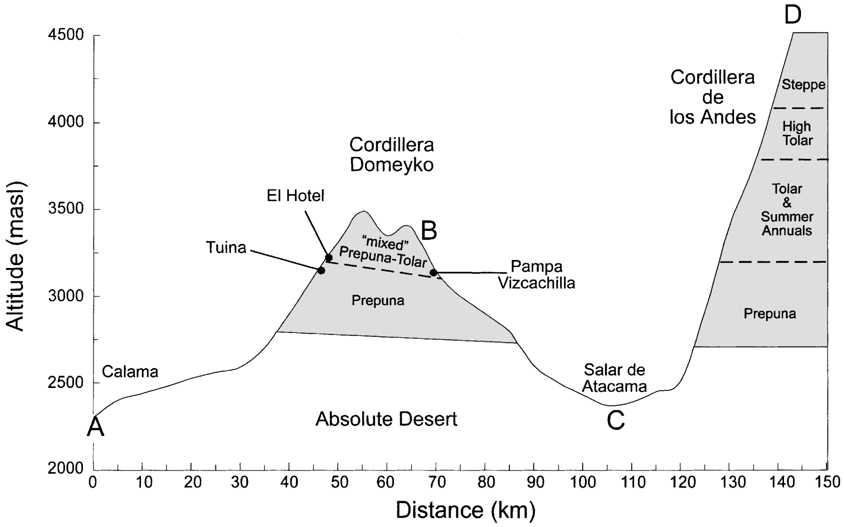

Fig. 2. Vegetation zones across a generalized east–west transect through the Cordillera Domeyko and the western Andean slope. Letters ABCD are keyed to Fig. 1. Midden sites are shown for comparisons to where modern vegetation zones are today. Unshaded areas correspond to zones devoid of vegetation at present.

2500 m, 20–40 mm at 2500–3000 m, 40–65 mm at 3000–3500 mm and 65–200 mm at 3500–4500 m. Mean annual temperature averages 10–15°C at 2000–3000 m (data from Dirección General de Aguas).

Seasonal precipitation in the central Atacama corresponds to the tail end of the South American Summer Monsoon (SASM) (Zhou and Lau, 1998). The SASM is produced by continental heating over the Altiplano and Gran Chaco during the austral spring and summer, modulated by the strength and size of the Bolivian High that forms in the upper troposphere (Lenters and Cook, 1995, 1997; Zhou and Lau, 1998). Modern climatology studies by Aceituno (1988), Garreaud (2000, 1999), Vuille (1999) and Garreaud et al. (this volume) describe El Niño-Southern Oscillation (ENSO) effects on interannual precipitation variability over the Altiplano. Because ENSO regulates the extent of atmospheric transport and convection over this region, different sensitivities should be evident in the eastern vs. western Cordilleras. Negative or warm ENSO phases (El Niño) are characterized by high-altitude westerly wind anomalies that inhibit moist air advection and convection over the western Altiplano. Conversely, positive or cold ENSO phases (La Niña) are characterized by a southward displacement of the Bolivian High and enhanced easterly circulation that produces greater advection and increased precipitation over the western Altiplano (Vuille, 1999). The link between modes of variability for the moisture source (the eastern Cordillera) vs. transport (and convection) to the western Altiplano is poorly understood.

2.3. Vegetation

Pronounced latitudinal and elevational climatic gradients lead to definable vegetation zones on the Pacific slope of the Andes. Five major zones or belts are distinguished: the coastal lomas; prepuna; tolar (or puna); Andean steppe; and subnival (near the upper vegetation limit and dominated by small cushion and rosette plants). The physical distribution of these vegetation belts and their association with climate are discussed in several references (Villagrán et al., 1981, 1983; Arroyo et al., 1988; Rundel et al., 1991; Latorre, 2002). Fig. 2 indicates the overall altitudinal distribution of vegetation zones along a transect that spans both mountain ranges. Fig. 3 compares our own floristic transects in the Cordillera Domeyko to those from the Andean slope at the same lat-

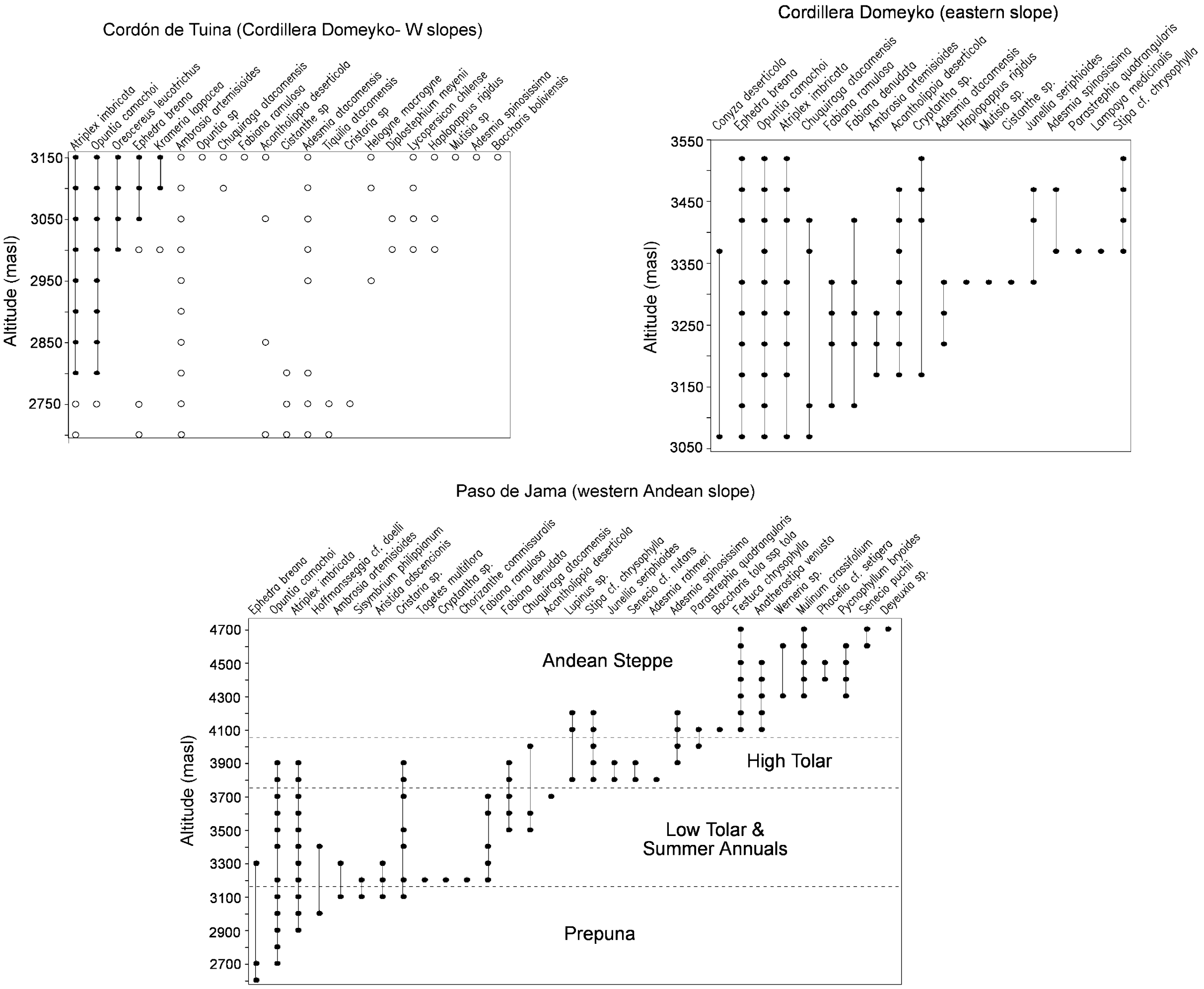

Fig. 3. Altitudinal plant ranges for three transects in the central Atacama Desert keyed to Fig. 1. Circles represent plants occupying azonal habitats whereas continuous lines represent a zonal distribution (see text). Species with zonal distributions are ordered based on first appearance along each survey.

itude. Vegetation zones in the Cordillera Domeyko are less distinct, physiognomically more homogeneous and less biodiverse than the Andean slope. This reflects the greater distance from the Andean crest, hence less precipitation, as well as a ‘double rainshadow’ present on the western slope of the Cordillera Domeyko.

Along the west-facing slopes of Cordón de Tuina, a diverse prepuna vegetation begins at ca. 2700 m, mostly in dry washes and other concave or level surfaces where water collects (these plants are termed ‘azonal’ in the ecological literature). Most perennial species of the Andean prepuna meet their lower limits along washes (Fig. 3, circles). These include *Lycopersicon chilense*, *Adesmia atacamensis*, *Tiquilia atacamensis*, *Ambrosia artemisioides* and *Haplopappus rigidus*. Hillslope or ‘zonal’ vegetation begins at ca. 2850 m and is dominated by the halophyte *Atriplex imbricata* and the cushion cactus *Opuntia camachoi*.

Columnar cacti, such as *Oreocereus leucotrichus*, appear at ca. 3050 m on hillslopes of the Cordón de Tuina. Although absent from Cordón de Tuina, *Echinopsis atacamensis*, another important species of columnar cacti, appears at ca. 3150 m on west-facing slopes of Cerros de Aiquina.

Ephedra breana (Ephedraceae) and *Krameria lappacea* (Krameriaceae) also appear at ca. 3100 m. Several tolar species begin to appear in dry washes and on hillslopes at ca. 3200 m, including *Fabiana ramulosa* (Solanaceae), *Baccharis boliviensis* and *Chuquiraga atacamensis* (both Asteraceae).

Zonal formations are more easily distinguished on east-facing slopes of the Cordillera Domeyko. Despite the dominance of prepuna assemblages along the entire transect up to ca. 3500 m (Fig. 3), tolar species show up at low densities at lower altitudes than on west-facing slopes (e.g. 3100 m vs. 3200 for *Fabiana ramulosa*). An isolated patch of *Parastrephia quadrangularis* (Asteraceae), a high tolar species (i.e. those that grow > 3800 m on Andean slopes), and *Lampaya medicinalis* (Verbenaceae) was also observed at 3300 m growing on a dry lake bed. Finally, a mixed community dominated by *Atriplex imbricata*, *Stipa chrysophylla*, *Ephedra breana* and *Opuntia camachoi* grows near the summits (∼3500 m) of the Cordillera Domeyko.

3. Methods

Fossil rodent middens are accumulations of organic (feces, plant, insect, and vertebrate) debris encased in hardened urine (amberat) ubiquitous in rock shelters, caves and crevices. Advantages of rodent midden analyses include the high taxonomic resolution (often to species), the limited origin of plant and animal material (generally within 100 m of the midden), the abundance of plant and fecal material for radiocarbon and other morphological, geochemical and genetic analyses, and the easy replicability within and across areas. Disadvantages include dietary selectivity of different rodents, occasional temporal mixing of midden assemblages, and discontinuous deposition. In effect, rodent middens represent individual snapshots of vegetation that have to be collated into series or chronologies for any particular site or area (Betancourt et al., 1990).

The majority of our middens from the northernmost outcrops at Cerros de Minta and Cerros de Aiquina (Fig. 4A,E) were collected underneath boulders and outcrops of Cretaceous breccias and conglomerates. Middens from Quebrada Chiquinaputo (Fig. 4B) were found within crevices and shelters formed in loosely consolidated Plio/Pleistocene alluvial sediments. Other middens were also found in the upper Paleozoic breccias that commonly outcrop along the Cordón de Tuina (Fig. 4C) and are locally abundant along isolated ignimbrite outcrops of El Hotel and Pampa Vizcachilla (Fig. 4D,F).

Middens were soaked in 10-l buckets of water for 2–3 weeks to dissolve urine (amberat), wet-sieved with a No. 20 mesh (0.825 mm) and placed in a drying oven at 50–60°C for 3 days. Dried middens were weighed, quantified for grass abundance, and sorted for plant macrofossils as described in Latorre et al. (2002). Most of the middens collected in the Atacama were made either by vizcachas (*Lagidium viscacia*, Chinchillidae) or leaf-eared mice (*Phyllotis* spp., Sigmodontinae). Both species usually have foraging areas < 100 m (Pearson, 1948; Pearson and Ralph, 1978). Ecological studies point to a generalized diet for both vizcachas and leaf-eared mice (Pearson, 1948; Pizzimenti and De Salle, 1980), and this is confirmed in our own analyses of modern middens. At midden site Cordón de Tuina 386, we found little difference in the composition of a modern vizcacha midden and an inventory of plants sampled within a 500-m radius on two successive late summers (Table 1). We feel that fossil rodent midden assemblages faithfully record local vegetation at the time the midden was formed, and are thus confident in interpreting paleovegetation and paleoclimates in terms of modern vegetation distributions described here and elsewhere (Villagrán et al., 1981, 1983; Latorre, 2002).

Between 3 and 10 g of feces from each midden were submitted for bulk dates at Geochronology Laboratories, Boston, MA, USA. We used accelerator mass spectrometry (AMS) in cases of insufficient material for bulk dates, or when contamination with younger materials was suspected. AMS targets pre-treated on our vacuum line at the Desert Laboratory in Tucson were then measured by the University of Arizona-NSF Accelerator Facility. All radiocarbon ages were calibrated with the Intcal98 calibration curve, using

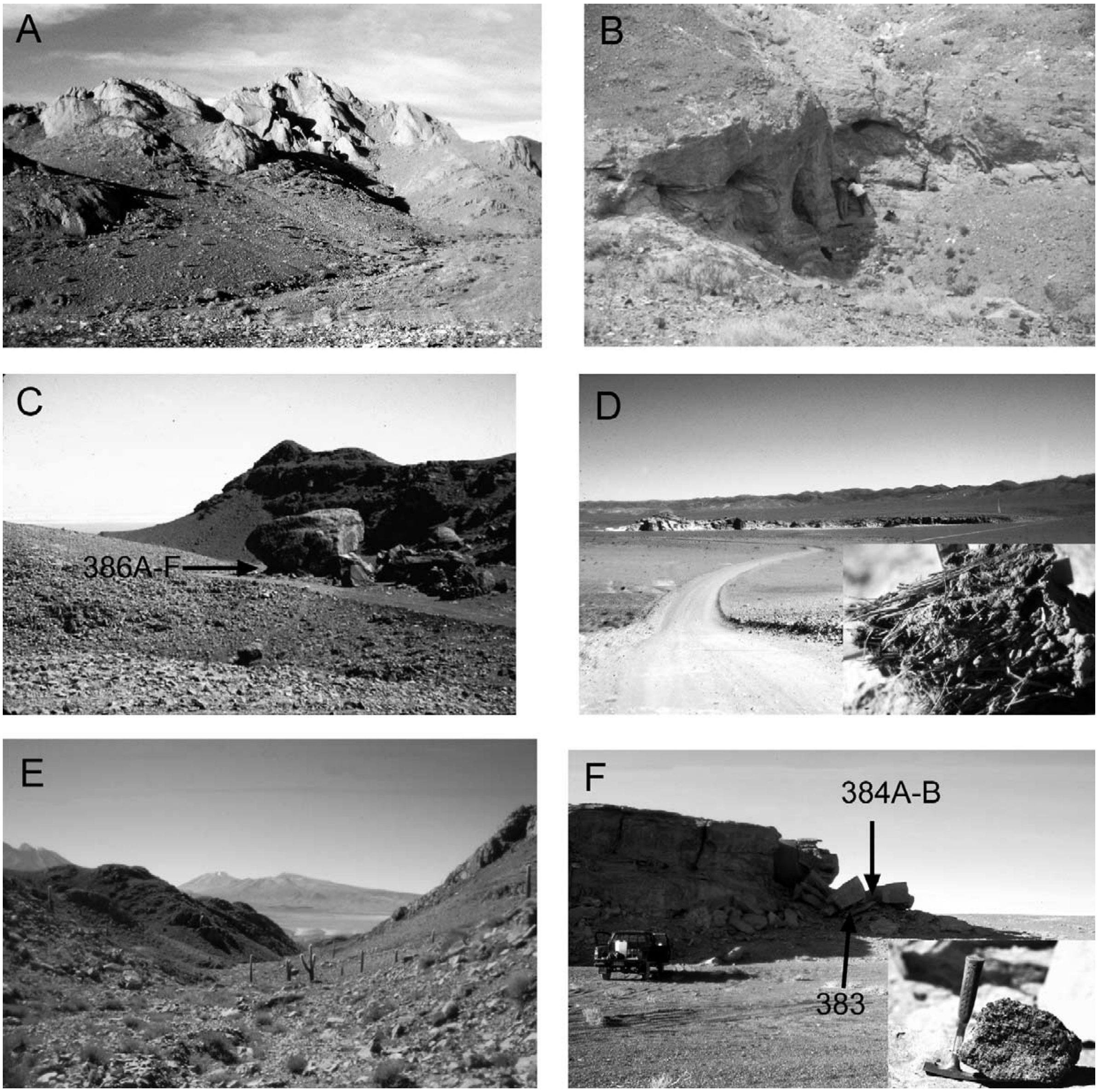

Fig. 4. Photographs of midden localities. (A) Cerros de Aiquina, viewed from the west. (B) Quebrada Chiquinaputo midden localities within loosely consolidated Plio/Pleistocene conglomerates. (C) Cordón de Tuina looking towards the northwest with arrow indicating large rockshelter with middens 386A–F. Inset: Grassy midden CdT 386B with AMS ^{14}C dates on grass of 11.2 ka. (D) Pampa Vizcachilla ignimbrite outcrop, view is towards the west. Inset: Grassy midden PV 402A ^{14}C-dated at 13 ka. (E) Cerros de Minta at 3300 m, looking towards the west to the Calama basin. Columnar cacti are specimens of *Echinopsis atacamensis*. (F) El Hotel ignimbrite locality with truck for scale. Arrows indicate where middens EH 383 and 384A-B were found. Inset: Large piece of midden EH 384B ^{14}C-dated at 13.2 ka.

Method A (ranges with intercepts) from Calib 4.3 (Stuiver and Reimer, 1993). A 24-yr Southern Hemisphere correction was applied to all dates. Radiocarbon ages reported here are in calendar thousands of years before 1950 (ka BP).

Plant macrofossils were hand-sorted and identified to the highest taxonomic level possible and each taxon was quantified using a relative abundance index where 0 = absent, 1 = rare, 2 = common and 3 = dominant (see Latorre et al., 2002). Macrofossil abundance was plotted with Tilia 2.0 and Tiliagraph software (Grimm, 1991–1993). Grass abundance was measured using a point occurrence method using a 120-cell rectangular grid overlain on a sorting tray. A sediment matrix splitter was used to randomly segregate 100 ml of plant debris from each washed and dried midden. Midden debris was then spread uniformly across a rectangular grid with 120 cells of 1 × 1 in (~6.45 cm^2). Percent grass abundance was calculated as the ratio of cells out of 120 where grass blades, florets or seeds were identified (i.e. ‘hits’ on the grid).

4. Results

4.1. Radiocarbon dating

Temporal coverage was quite variable at the six localities studied, where we collected a total of 44 ^{14}C-dated middens (Table 2; Fig. 5). We managed to find late glacial–early Holocene middens at Cerros de Aiquina, Cordón de Tuina and Pampa Vizcachilla and El Hotel, but not at Cerros de Minta and Quebrada Chiquinaputo. In general, midden ages clustered in the late glacial–early Holocene and the late Holocene. The largest cluster of dates occurs between 13.5 and 9 ka.

4.2. Grass abundance

Between 13.4 and 9.4 ka, grass percentages are on average > 50% at all localities, with conspicuous drops at 13.1 and 11.5–11.2 ka (Fig. 6a). Percentages remain ≤ 10% between 9.4 and 7.6 ka, excluding a brief increase to 47% at 8.4 ka at Cerros de Aiquina. An abrupt increase in percentages occurs at 7.6 ka, with values remaining above 40% until 3.2 ka. This middle Holocene interval was punctuated by a brief drop to 3% grass at 5.1 ka at Cordón de Tuina. Modern grass abundance levels (< 10%) were established at 2.8 ka, with a slight increase between 1.8 and 1.2 ka at Cordón de Tuina, Cerros de Minta and Pampa Vizcachilla. By far the most surprising patterns are the sustained, pronounced decreases in grass abundance that begin at 10.2 and at 3.4 ka.

4.3. Plant macrofossil assemblages

A total of 59 taxa were identified to genus or species from seeds, achenes, florets, fruits, leaves or stems (Table 3; Figs. 7–10). A summary of the pa-

Table 1
Comparison between vegetation collected by the authors and that present in an active *Lagidium* midden at the Cordón de Tuina 386 site

Taxa	Collected March, 1998	CdT 386-modern
Ambrosia artemisioides	X	X
Atriplex imbricata	X	X
Cistanthe spp.	X	X
Chorizanthe commisuralis		X
Cryptantha spp.	X	X
Diplostephium meyenii	X	X
Ephedra breana	X	X
Lycopersicon chilense	X	
Tagetes multiflora		X
Opuntia camachoi	X	X
Oreocereus leucotrichus	X	
Total	9	9

Table 2
Site location and radiocarbon dates for the 44 middens used in this study

Midden field number		Radiocarbon lab number	Radiocarbon date (^{14}C yr BP)	δ^{13}C (PDB)	Calendar age (yr BP) 1σ	Midpoint	Grass (%)	Number of taxa	Elevation (masl)	Midden agent	Slope aspect
(1) Quebrada Chiquinaputo											
1	QC 377A	GX-27818	250 ± 70	−20.6	312 (290) 3	290	20	18	3043	*Phyllotis*	NW
2	QC 377C	GX-27819	340 ± 50	−21.2	463 (422, 398, 318) 304	398	0	12	3043	*Phyllotis*	NW
3	QC 376	GX-27817	420 ± 60	−20.5	511 (478) 326	478	0	17	3046	*Phyllotis*	NW
(2) Cerros de Minta											
4	CdM 485	GX-27823	1860 ± 60	−24.2	1863 (1815, 1797, 1775, 1757, 1739) 1706	1775	40	19	3300	*Lagidium*	S
5	CdM 484	GX-27822	2490 ± 70	−24.2	2728 (2705, 2647, 2489, 2474) 2357	2489	0	13	3300	*Lagidium*	SW
6	CdM 482A	GX-27821	3060 ± 70	−22.8	3348 (3314, 3313, 3246, 3220, 3214) 3082	3246	37	8	3250	*Lagidium*	S
7	CdM 481B	GX-25658	4070 ± 80	−22.5	4788 (4523, 4459, 4452) 4419	4459	49	16	3250	*Lagidium*	E
(3) Cerros de Aiquina											
8	CdA 483B	GX-25655	2780 ± 80	−22.9	2949 (2850) 2775	2850	7	19	3150	*Lagidium*	S
9	CdA 458	GX-26622	5920 ± 90	−23.7	6848 (6723, 6697, 6682) 6575	6697	52	30	3174	*Lagidium*	ENE
10	CdA 457A	GX-25654	6720 ± 110	−23.5	7664 (7571) 7439	7571	97	26	3120	*Lagidium*	NW
11	CdA 457B	GX-26624	6780 ± 60	−24.1	7668 (7609, 7598, 7590) 7572	7598	10	12	3120	*Lagidium*	SSW
12	CdA 483C	GX-25656	7710 ± 210	−22.6	8645 (8424) 8221	8424	47	21	3150	*Lagidium*	S
13	CdA 456	GX-26621	8230 ± 70	−24.1	9396 (9241, 9219, 9188, 9175, 9131) 9029	9188	9	23	3150	*Lagidium*	S
14	CdA 483A	GX-26625	8470 ± 120	−23.4	9535 (9485, 9476, 9474) 9305	9476	67	16	3150	*Lagidium*	S
15	CdA 455B	GX-26623	8720 ± 90	−24.6	9888 (9676, 9671, 9660, 9648, 9628, 9608, 9603) 9547	9648	29	26	3120	*Lagidium*	WNW
16	CdA 483D	GX-25657	10030 ± 260	−22.6	12100 (11546, 11510, 11403, 11390, 11341) 11175	11403	15	16	3150	*Lagidium*	S
(4) Cordón de Tuina											
17	CdT 386-m	modern	modern		–	0	0	0	9	3190	
18	CdT 391A	GX-25418	1100 ± 80	−22.3	1060 (967) 928	967	0	12	3150	*Lagidium*	N
19	CdT 391C1	GX-25419	1240 ± 100	−22.9	1265 (1170, 1156, 1153) 990	1156	30	15	3150	*Lagidium*	N
20	CdT 388	GX-24208	4540 ± 100	−18.8	5317 (5282, 5161, 5138, 5103, 5074) 4977	5138	3	19	3173	*Lagidium*	SW
21	CdT 386F	GX-24878	8710 ± 130	−24	9907 (9656, 9652, 9626, 9618, 9601, 9584, 9564, 9564) 9533	9618	0	18	3190	*Lagidium*	SW
22	CdT 387-2	GX-26748	8940 ± 70	−24.3	10188 (10150, 10044, 9987, 9975) 9915	10044	81	20	3150	*Lagidium*	S
23	CdT 386B	GX-24204	9025 ± 155	−23.8	10356 (10189) 9914	10189	98	23	3190	*Lagidium*	SW
	CdT 386B	AA-44217	9754 ± 67	−25.0	11199 (11171) 11125	11171	–	–	date on individual grass blades		
24	CdT 389C	GX-24210LS	9630 ± 95	−25.8	11166 (11085, 11081, 11072, 10937, 10869) 10703	11072	60	14	3180	*Lagidium*	NW

Table 2 (*Continued*).

Midden field number		Radiocarbon lab number	Radiocarbon date (^{14}C yr BP)	$\delta^{13}C$ (PDB)	Calendar age (yr BP) 1σ	Midpoint	Grass (%)	Number of taxa	Elevation (masl)	Midden agent	Slope aspect
25	CdT 386C	GX-24205	9630 ± 140	−23.8	11176 (11085, 11081, 11072, 10937, 10869) 10692	11072	89	10	3190	*Lagidium*	SW
26	CdT 389A	GX-24209	9800 ± 160	−23.1	11296 (11192) 10875	11192	10	20	3180	*Lagidium*	NW
27	CdT 386A	GX-24203	10140 ± 160	−24.4	12266 (11691, 11665, 11662) 11262	11655	98	30	3190	*Lagidium*	SW
28	CdT 391C2	GX-24211	10280 ± 150	−23.2	12573 (12069, 12036, 11957) 11645	12036	88	14	3150	*Lagidium*	N
(5) El Hotel–Paso Barros Arana											
29	EH 383	GX-24200LS	8320 ± 90	−23.9	9468 (9397, 9386, 9369, 9360, 9345, 9343, 9296) 9132	9360	8	20	3219	*Lagidium*	SE
30	EH 384B	GX-24202LS	11190 ± 120	−24.4	13190 (13148) 13006	13148	5	16	3219	*Lagidium*	W
31	EH 384A	GX-24201	11480 ± 170	−23.1	13791 (13438) 13168	13438	74	14	3219	*Lagidium*	W
(6) Pampa Vizcachilla											
32	PV 404	GX-24913	220 ± 65	−24.5	302 (281, 169, 154) 2	169	4	17	3125	*Lagidium*	E
33	PV 405	GX-24912	435 ± 105	−24.2	533 (498) 314	498	2	11	3125	*Lagidium*	E
34	PV 428A	GX-24913	660 ± 65	−23.0	661 (647, 582, 567) 549	582	1	12	3125	*Lagidium*	E
35	PV 434B	GX-24980	895 ± 70	−23.0	911 (785, 783, 763) 694	783	2	9	3125	*Lagidium*	E
36	PV 428B1	GX-24938	1270 ± 70	−23.5	1266 (1175) 1064	1175	24	13	3125	*Lagidium*	E
37	PV 429B	GX-24939	2005 ± 75	−23.5	1999 (1925, 1906, 1903) 1832	1906	6	13	3125	*Lagidium*	E
38	PV 429A	GX-24979	2130 ± 75	−24.0	2295 (2105, 2081, 2066) 1953	2081	3	12	3125	*Lagidium*	E
39	PV 434A	GX-25044	3040 ± 80	−23.2	3341 (3236, 3232, 3211) 3078	3232	23	12	3125	*Lagidium*	E
40	PV 427	GX-24830	3100 ± 140	−21.8	3447 (3325, 3285, 3269) 3078	3285	63	22	3125	*Phyllotis*	E
41	PV 431	GX-24915	3230 ± 270	−22.4	3807 (3441, 3427, 3404) 3078	3427	78	22	3125	*Phyllotis*	E
42	PV 426	GX-24937	5500 ± 160	−22.8	6409 (6286) 6002	6286	100	26	3125	*Phyllotis*	E
43	PV 402B	GX-24874	10870 ± 180	−25.9	13108 (12905) 12654	12905	98	9	3125	*Lagidium*	E
44	PV 402A	GX-24875	10960 ± 180	−24.6	13143 (12974) 12679	12974	26	11	3125	*Lagidium*	E

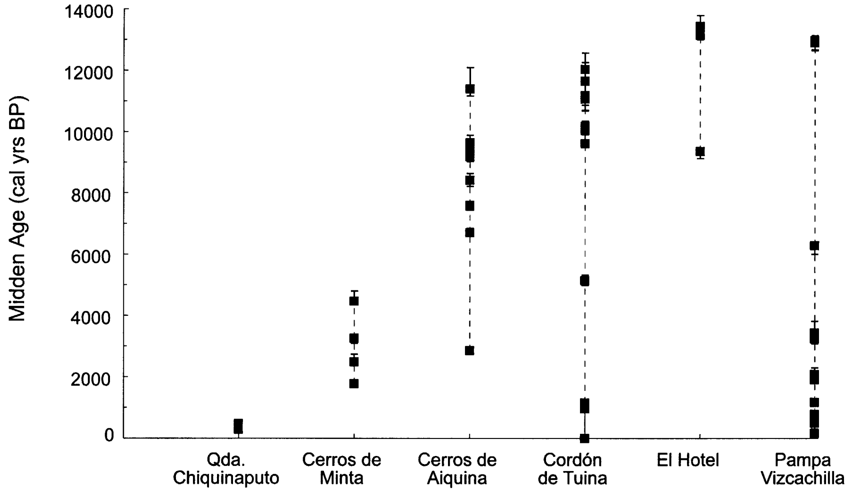

Fig. 5. Individual time series (in calendar years) for all six midden sites based on midden radiocarbon dates (interval is at 1σ).

leoclimate implications is given in Table 4. The overall trend in species richness at all the localities except Pampa Vizcachilla and Cerros de Minta is a general decrease from the early–middle Holocene towards the present. Although all of these taxa are found in northern Chile, many are currently absent from the midden sites (i.e. extralocal taxa).

The combined macrofossils from Cerros de Ai-

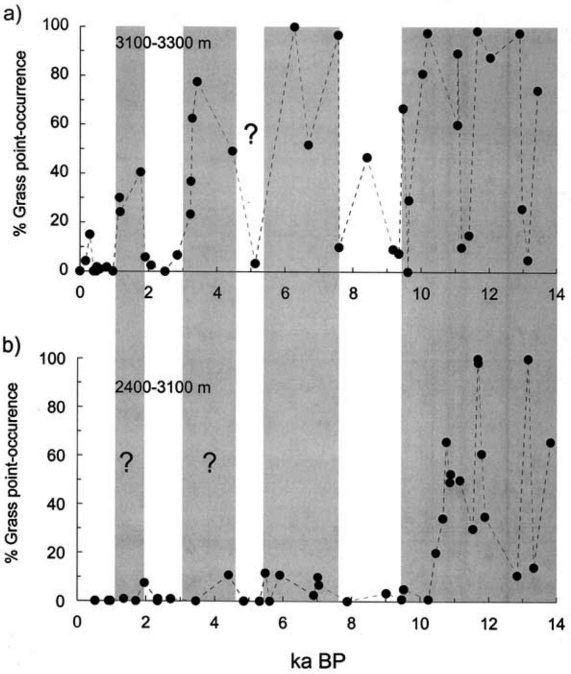

Fig. 6. Comparison of high- (a) and low- (b) elevation grass abundance (%) calculated from grass point occurrence obtained from a total of 83 middens ($n = 44$ in a; $n = 39$ in b). Shading reflects intervals wetter than today whereas white backgrounds are intervals as dry or drier than today (a question mark signifies lack of replication between records).

Table 3
List of 59 taxa identified from macrofossils present in Cordillera Domeyko middens

Taxon	Family	Plant part identified	Physiognomic affinity
Gymnospermae			
Ephedra sp.	Ephedraceae	seeds, bark	prepuna perennial
Angiospermae–Dicotyledons			
Ambrosia artemisioides Meyen et Walp.	Asteraceae	pseudoachenes, leaves	prepuna perennial
Baccharis boliviensis (Wedd.) Cabrera	Asteraceae	leaves	tolar
Baccharis tola Phil. ssp. *tola*	Asteraceae	leaves	tolar
Bidens aff. *pilosa* L.	Asteraceae	achenes	
Bidens aff. *pseudocosmos* Sherff.	Asteraceae	achenes	
cf. *Conyza deserticola* Phil.	Asteraceae	achenes	prepuna annual
Chuquiraga atacamensis Kuntze	Asteraceae	achenes, leaves	tolar perennial
Diplostephium meyenii Wedd.	Asteraceae	leaves	prepuna/tolar perennial
Helogyne macrogyne (Phil.) B.L. Rob.	Asteraceae	achenes	prepuna/tolar perennial
Parastrephia quadrangularis (Meyen) Cabrera	Asteraceae	leaves	high tolar perennial
Schkuhria multiflora Hook. et Arn.	Asteraceae	achenes	tolar annual
Senecio aff. *atacamensis* Phil.	Asteraceae	leaves	tolar perennial
Tagetes multiflora Kunth	Asteraceae	achenes	tolar annual
Urmenetea atacamensis Phil.	Asteraceae	achenes	prepuna annual
Cryptantha diffusa (Phil.) I.M. Johnst.	Boraginaceae	nutlets	prepuna annual
Cryptantha hispida (Phil.) Reiche	Boraginaceae	nutlets	prepuna annual
Cryptantha limensis (A. DC.) I.M. Johnst.	Boraginaceae	nutlets	prepuna annual
Cryptantha phaceloides (Clos) Reiche	Boraginaceae	nutlets	prepuna annual
Pectocarya dimorpha (I.M. Johnst.) I.M. Johnst.	Boraginaceae	nutlets	
Tiquilia atacamensis (Phil.) A.T. Richardson	Boraginaceae	nutlets, leaves	prepuna annual
Lepidium sp.	Brassicaceae	silicules	prepuna/tolar annual
Sisymbrium philippianum I.M. Johnst.	Brassicaceae	siliques	prepuna annual
Echinopsis atacamensis (Phil.) Friedrich et G.D. Rowley	Cactaceae	seeds	prepuna/tolar perennial
Opuntia camachoi Espinosa	Cactaceae	seeds	prepuna/tolar perennial
Opuntia ignescens Vaupel	Cactaceae	seeds	tolar perennial
Opuntia sphaerica C.F. Först	Cactaceae	seeds	prepuna perennial
Oreocereus sp.	Cactaceae	seeds	prepuna/tolar perennial
Hoffmannseggia sp.	Caesalpinaceae	seeds, leaves	prepuna perennial
Spergularia sp.	Caryophyllaceae	seeds	tolar
Atriplex imbricata (Moq.) D. Dietr.	Chenopodiaceae	seeds, leaves, bark	prepuna perennial
Euphorbia sp.	Euphorbiaceae	seeds, flower bracts	prepuna/tolar perennial
Adesmia atacamensis Phil.	Fabaceae	leaves	prepuna perennial
Adesmia spp.	Fabaceae	seeds	prepuna and tolar perennials
Phacelia sp.	Hydrophyllaceae	seeds	prepuna perennial
Krameria lappacea (Dombey) Burdet et B.B. Simpson	Krameriaceae	fruits	prepuna/tolar perennial
Cristaria spp.	Malvaceae	seeds	Annual
Tarasa operculata (Cav.) Krapov.	Malvaceae	seeds	prepuna subshrub
Plantago hispidula Ruiz et Pavon	Plantaginaceae	flowers	prepuna/tolar annual
Gilia cf. *glutinosa* Phil.	Polemoniaceae	flower bracts	prepuna/tolar annual
Chorizanthe commissuralis J. Remy	Polygonaceae	fruits	prepuna/tolar annual
Cistanthe spp.	Portulacaceae	seeds, leaves, stems	prepuna annuals
cf. *Galium* sp.	Rubiaceae	seeds	
Exodeconus integrifolius (Phil.) Axelius	Solanaceae	seeds	prepuna annual
Fabiana spp.	Solanaceae	stems	tolar perennial
Lycopersicon chilense Dunal	Solanaceae	seeds, leaves	prepuna perennial
Acantholippia deserticola (Phil. Ex F. Phil.) Moldenke	Verbenaceae	seeds, leaves	prepuna perennial
Junellia seriphioides (Gillies et Hook) Moldenke	Verbenaceae	seeds	tolar perennial
Angiospermae–Monocotyledonae			
Anatherostipa venusta (Phil.) Peñail.	Poaceae	florets	steppe perennial
Aristida adscensionis L. var. *bromoides* (Kunth) Henrard	Poaceae	florets	tolar C_4 annual

Table 3 (*Continued*).

Taxon	Family	Plant part identified	Physiognomic affinity
Bouteloua simplex Lag.	Poaceae	florets	tolar C_4 annual
Bromus catharticus Vahl.	Poaceae	florets	
Munroa cf. *andina* Phil.	Poaceae	florets	tolar C_4 annual
Munroa decumbens Phil.	Poaceae	florets	tolar C_4 annual
Nassella arcuata (R.E. Fries) Torres	Poaceae	florets	steppe perennial
Nassella nardoides (Phil.) Barkworth	Poaceae	florets	steppe perennial
Nassella pubiflora (Trin. et Rupr.) E. Desv.	Poaceae	florets	steppe perennial
Nassella pungens E. Desv.	Poaceae	florets	lomas perennial
Stipa chrysophylla E. Desv.	Poaceae	florets	steppe perennial

quina–Quebrada Chiquinaputo (Fig. 7) clearly demonstrate this overall trend. Maximum species richness was reached at 9.5 and 7.6–6.7 ka. The oldest midden in this series, dated at 11.4 ka, has low species richness, low grass abundance, and common plants are the cacti *Opuntia camachoi*, *Opuntia sphaerica* and *Atriplex imbricata*. Macrofloras for middens dated 9.7–9.5 ka were much more diverse and characterized by steppe, tolar and numerous summer annuals. Prominent among these are *Nassella arcuata*, *Nassella pubiflora* and *Junellia seriphioides*. Except for *N. pubiflora*, these taxa disappear from the record at 9.2–8.4 ka although many summer annuals and cacti persist in the record. Steppe and tolar taxa reappear in middens dated at 7.6–6.7 ka and species richness reaches a maximum of 30 taxa at 6.7 ka. One curious pattern is the disappearance of 'other' taxa (including species with coastal affinities) from the record after 6.7 ka. Macrofloras from a midden dated at 2.8 ka are considerably less diverse and contain mostly cacti and a few summer annuals. These species were present to a lesser extent in the Quebrada Chiquinaputo middens, 10 km from the Cerros de Aiquina localities. Dated at 0.48–0.3 ka, these middens have modern floras with the dominance of prepuna perennials and annuals.

A similar pattern exists at Cordón de Tuina (Fig. 8). Macrofossil species were richest at 11.6–10.0 ka. These assemblages included numerous steppe and tolar species and summer annuals. Among these are high tolar species such as *Baccharis boliviensis* and *Baccharis tola* ssp. *tola*. The steppe grass *Anatherostipa venusta* is today found above 3800 m on the western Andean slope and is not present anywhere in the Cordillera Domeyko (implying an altitudinal descent of at least 650 m). In comparison, the oldest midden dated at 12.0 ka has a reduced species richness with no steppe grasses and only one tolar species, *B. tola* ssp. *tola*. Macrofloras change abruptly at 9.6 ka and steppe, tolar and 'other' taxa disappear along with most summer annuals. Assemblages were dominated by the columnar cactus *Echinopsis atacamensis* (presently absent from this area) and the common prepuna shrub *Ambrosia artemisioides*. Cacti become less prominent and summer annuals increase in a 5.1-ka midden dominated by *Atriplex imbricata*. These assemblages are similar to those present in the late Holocene middens at 1.1–0.0 ka and in the modern vegetation (see Table 1).

Macrofossil assemblages from Pampa Vizcachilla (Fig. 9) exhibit a slightly different trend through time than the previous two records. Overall, macrofloras were more stable throughout this record. Most prominent was the presence of the high tolar species *Parastrephia quadrangularis* and *Baccharis tola* ssp. *tola* and the coastal lomas species *Nassella pungens* in only the oldest two middens at 13.0–12.9 ka. Today, these species occur locally some 300 m higher in the Cordillera Domeyko. These late glacial middens also have limited representatives of the more arid floras from the prepuna belt. Species richness reaches a maximum of 26 taxa during the middle Holocene at 6.2 ka and of 22 species between 3.4 and 3.3 ka. The 6.3-ka midden has two species of steppe grasses, numerous cacti and summer annuals. Prepuna species such as *Atriplex imbricata* and *Ephedra* become very common and/or abundant for the remainder of this series. *Nassella ar-*

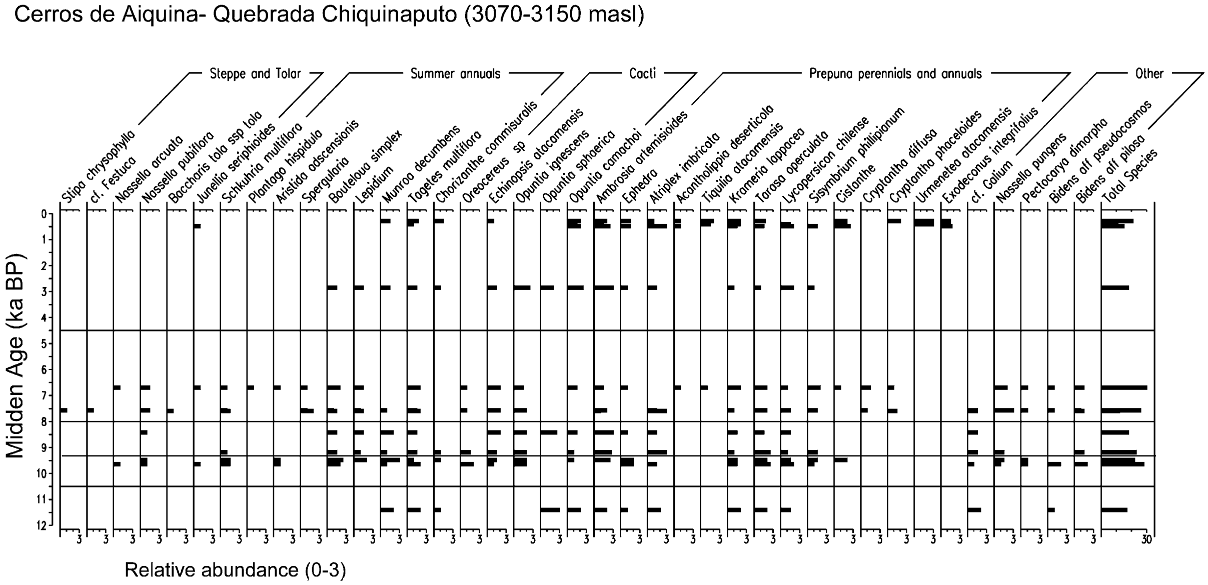

Fig. 7. Combined macrofossil relative abundance diagram for the Cerros de Aiquina and Quebrada Chiquinaputo localities (12 middens). Major vegetation changes are denoted by horizontal lines. Relative abundance scale is: 0 = absent; 1 = rare; 2 = common; 3 = dominant.

cuata disappears from the record after 3.4 ka although *Stipa chrysophylla* (which was found growing along a small river valley nearby) remains present until recently. Both middle and late Holocene middens (between 2.1 and 0.17 ka) indicate that numerous summer annuals have been dominant since at least 6.3 ka. The tolar shrubs *Fabiana* spp. and *Chuquiraga ataca-*

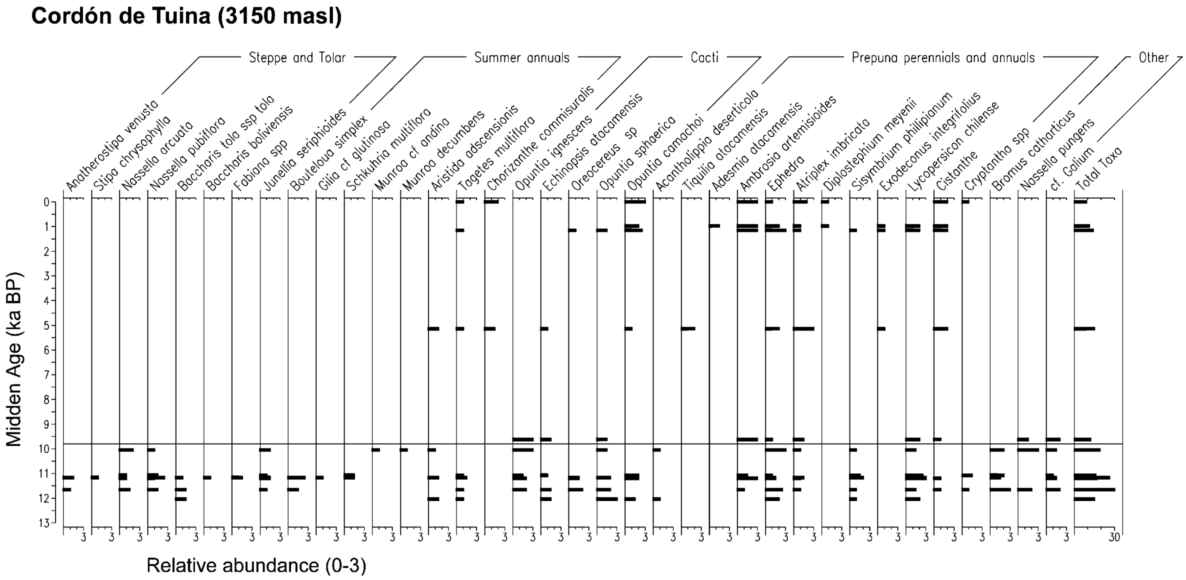

Fig. 8. Macrofossil relative abundance diagram for the Cordón de Tuina locality (12 middens). Note major vegetation break between 10 and 9.6 ka. Scale as in Fig. 7.

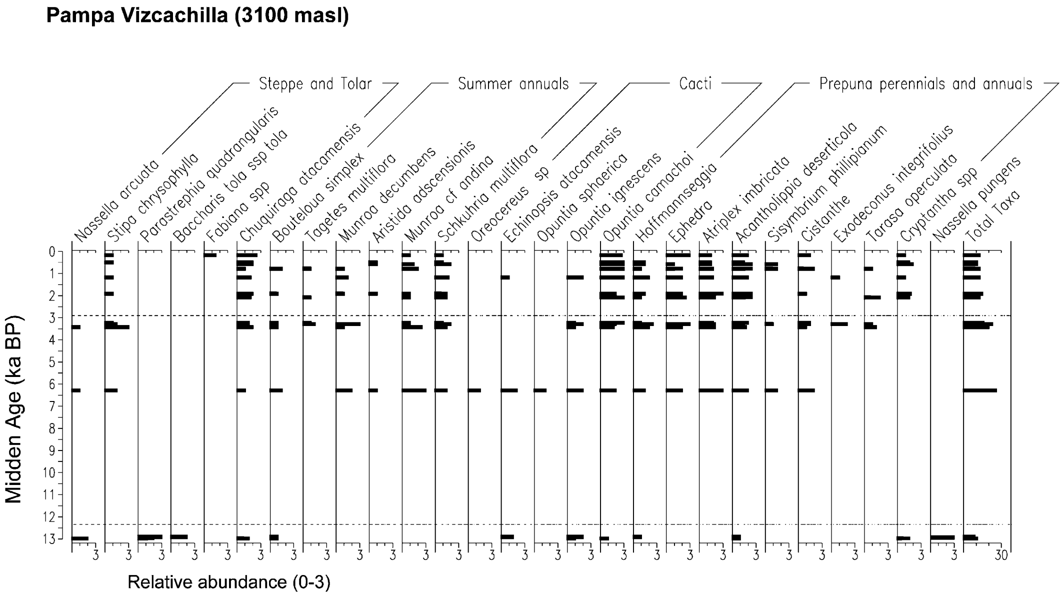

Fig. 9. Macrofossil relative abundance diagram for the Pampa Vizcachilla locality (13 middens). Breaks and scale as in previous figures.

mensis were found growing near the middens today. In fact, late Holocene middens indicate that *Fabiana* may be a recent arrival and that *Chuquiraga* has become dominant in the area only recently. The dominant perennials at present, *Opuntia camachoi* and *Acantholippia deserticola*, only became locally important starting at 3.2 ka.

The last two midden series are from west- and east-facing slopes along the higher elevations of the Cordillera Domeyko (Fig. 10). Although sparse, these records represent the late glacial–early Holocene transition at El Hotel and the middle to late Holocene transition at Cerros de Minta. A diverse assemblage consisting of the steppe grass *Nassella arcuata* and several tolar species occurred at the west-facing site El Hotel between 13.4 and 13.1 ka. This assemblage contrasts with that present in a midden dated at 9.4 ka, in which all these taxa disappear, including the grass *Nassella pungens*. This younger midden presents mostly modern assemblages, as well as abundant summer annuals.

At the east-facing site Cerros de Minta, a midden from 4.5 ka records the presence of *Nassella arcuata*, numerous summer annuals and maximum species richness (20 taxa). *Nassella arcuata* is not recorded in any of the younger middens collected here and several of the summer annuals disappear as well. Younger middens reflect the dominance of *Opuntia camachoi* and *Echinopsis atacamensis*, as well as *Stipa chrysophylla*, a steppe grass found near Cerros de Minta today. The coastal lomas grass *Nassella pungens* occurs here at 1.8 ka, the youngest occurrence for any of the middens described in this paper.

5. Discussion

Grass abundance values, which in the Atacama reflect primary productivity and thus track seasonal precipitation amounts (Meserve and Glanz, 1978; Latorre et al., 2002), are highest at 13.5–9.4 ka, 7.6–6.3 ka, 4.3–3.0 ka and 1.8–1.2 ka. Wet phases are also inferred from high species richness and presence of extralocal taxa, particularly those from higher elevations, specifically at 13.5–9.6 ka, 7.6–6.3 ka, 5.1–3.2 ka and 2.8–1.2 ka. The chronology of wet and dry phases as inferred from the macrofloras (Figs. 5–8, Table 4) is generally in good agreement with that inferred from midden grass abundance for the last 13.5 ka (Fig. 6), de-

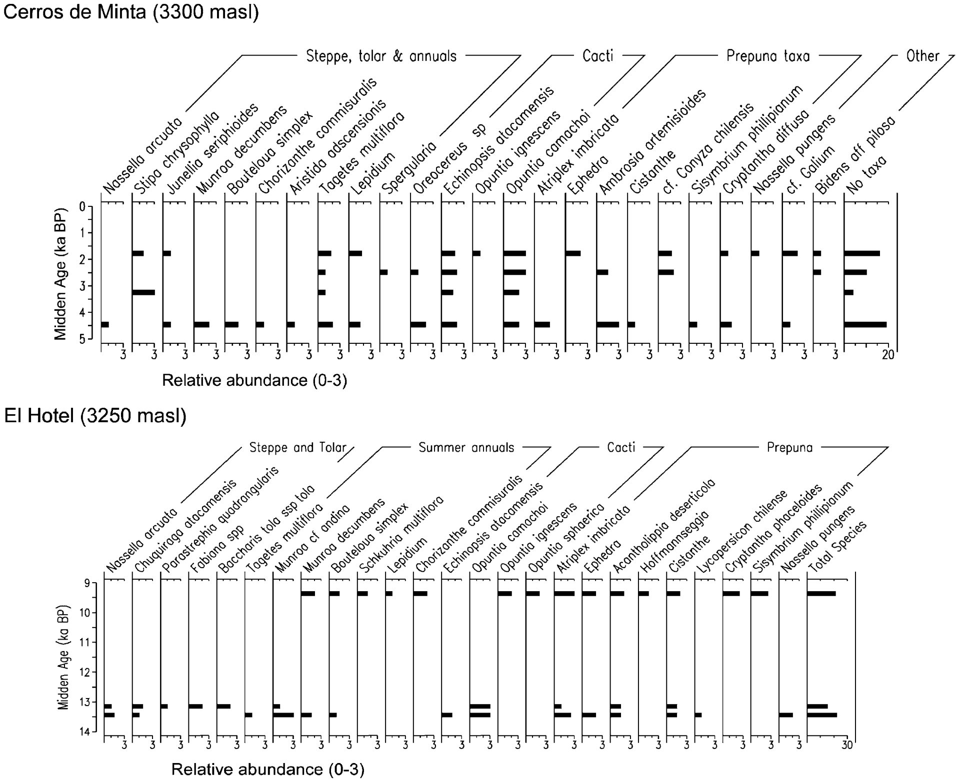

Fig. 10. Macrofossil relative abundance diagrams for the Cerros de Minta and El Hotel localities (total seven middens). Scale as in previous figures.

spite local site differences in terms of aspect, elevation and microclimate.

5.1. Late glacial to early Holocene plant communities

Overall, late glacial communities present at Cordón de Tuina, Cerros de Aiquina, Pampa Vizcachilla and El Hotel were diverse and dominated by the steppe grasses *Nassella arcuata* and *Nassella pubiflora*, as well as numerous summer annuals and cacti. *Nassella arcuata* and *N. pubiflora* are now very rare in the central Atacama, but more common in northernmost Chile (lat. 18°S) and the Bolivian Altiplano (Matthei, 1965; Rojas, 1994) where precipitation is much greater today. The tolar shrubs *Fabiana* spp. and *Junellia seriphioides* were also common during the late glacial at most sites. The high tolar species (that presently grow > 3500 m on the Andean slope) *Parastrephia quadrangularis* and *Baccharis tola* ssp. *tola* were common at higher (El Hotel) and east-facing (Pampa Vizcachilla) sites. Several other extralocal taxa were also present, such as *Nassella pungens*, cf. *Galium*, *Bidens* spp., and *Bromus catharticus*. Notably, the perennial grass *N. pungens* is found today only at coastal lomas localities (Rundel et al., 1996; Marticorena et al., 1998). At present, we can only speculate on the presence of this species in the midden record. One possibility is that it came up from the coast along dry river valleys that might have been more effective corridors for migrations during wetter times in the past. The presence of steppe and high tolar taxa implies a minimum altitudinal descent of 300 m either from the summits of the Cordillera Domeyko (ca. 3500 m) or from the western Andean slope. These descents in turn imply a precipitation increase of at least double the amount that falls today (from 40–50 mm to 80–100 mm).

Table 4
Paleoclimatic implications from macrofloras of 44 middens collected from the Cordillera Domeyko, Central Atacama Desert

Interval (ka)	Number of middens analyzed	Description	Inferred paleoclimate
0.0–1.0	9	Modern assemblages dominated by prepuna taxa. Species richness averages 15 taxa. Summer annuals relatively rare. *Stipa chrysophylla*, a steppe grass and tolar taxa are rare and found on east-facing slopes (e.g. Pampa Vizcachilla).	Present hyperarid climate.
1.2–2.8	7	Average 14 taxa. Cacti (several species), prepuna taxa and annuals are common at most localities. *Stipa chrysophylla* is present ~2.0 ka BP at higher elevations. Last appearance of *Nassella pungens*, a coastal species, at 1.9 ka BP.	Generally hyperarid with slightly wetter climate at 1.2–1.8 ka indicated by increases in grasses and cacti diversity at some localities.
3.2–5.1	6	Average 16 taxa. Abundant summer annuals, cacti and prepuna taxa. Two species of steppe grasses present in minor amounts at two east facing localities. Low species richness and plant assemblages similar to modern at 5.1 ka.	Generally wetter than today. Moisture was probably greatest near the youngest part of the interval. Possibly arid at 5.1 ka at Cordón de Tuina.
6.3–7.6	4	Average 23 taxa, the highest in the record. Characterized by numerous annuals. Three species of steppe grasses are present. A few tolar taxa are also present. Cacti and prepuna shrubs, notably *Atriplex imbricata*, are abundant. *Nassella pungens* is very abundant.	A wet interval. High diversity implies high plant cover. Presence of steppe grasses indicates rainfall greater than twice the present amount.
8.4–9.6	5	Average 20 taxa. Steppe and tolar taxa are almost completely absent. Cacti and prepuna shrubs are very abundant as well as summer annuals.	Aridity abruptly increased as evidenced by the disappearance of steppe and tolar taxa. The abundance of cacti, however, indicates rainfall greater than today.
9.6–11.7	8	Very diverse assemblages at most sites. Average 19 taxa. Steppe grasses include *Anatherostipa venusta*, *Nassella arcuata* and *Nassella pubiflora*. Abundant summer annuals and tolar shrubs. Prepuna shrubs and annuals present in low numbers.	The wettest interval in the record. Steppe grasses indicate large rainfall increases. Diverse assemblages without present-day analogues.
12.0–13.5	5	Average 13 taxa. Only appearance of *Parastrephia quadrangularis*, a high tolar species, in the record at two sites. Steppe grasses and other tolar taxa common. Few annuals and prepuna perennials.	Climate much wetter than today and possibly cooler as evidenced by lack of both summer and prepuna annuals.

Among the most prominent changes in the midden macrofloras was the sudden and abrupt disappearance of all tolar and steppe taxa between 10.0 and 9.6 ka at Cordón de Tuina, and between 9.5 and 9.2 ka at Cerros de Aiquina, the two most complete series for the time interval involved. These taxa had also disappeared from the El Hotel site (which is 100 m higher in elevation) by 9.4 ka. These species departures were accompanied by a large drop in grass abundance that occurred starting at 10.2 ka and culminated at 9.4 ka. Abrupt onset of a sustained drought is the most likely cause for reduced midden species richness and grass abundance that had occurred by at least 9.4 ka at all sites.

By 9.6 ka, a Cordón de Tuina midden reveals an extremely arid flora, as represented by the large decrease in species richness and the dominance of *Ambrosia artemisioides* (a 'type' species of the modern prepuna). Midden macrofloras remained impoverished between 9.2 and 8.4 ka at Cerros de Aiquina, the only site with a sequence of early Holocene middens (Figs. 5 and 8). Plant communities during this interval lacked steppe (save for the rare presence of *Nassella pubiflora* at 8.4 ka), tolar taxa, and many summer annuals, and were characterized instead by the dominance of prepuna shrubs, especially *Ambrosia artemisioides*, *Atriplex imbricata* and *Opuntia camachoi*.

5.2. Middle to late Holocene plant communities

Early Holocene drought conditions did not persist into the middle Holocene, as steppe (*Stipa chrysophylla*, *Nassella arcuata* and *Nassella pubiflora*) and tolar taxa (*Baccharis tola* ssp. *tola* and *Junellia seriphioides*) reinvaded the Cerros de Aiquina midden sites by 7.6 ka. In particular, the presence of *B. tola* ssp. *tola* implies an altitudinal descent of at least 350 m from the western Andean slopes where it is present today at altitudes > 3500 m. This was accompanied by a large increase in grass abundance similar to late Pleistocene percentages (Fig. 6). These taxa remained at Cerros de Aiquina until at least 6.7 ka. At Pampa Vizcachilla, *Nassella arcuata* and *Stipa chrysophylla* were present in a 6.3-ka midden. The large numbers of cacti and summer annuals present here and at Cerros de Aiquina largely account for the elevated species richness observed between 7 and 6 ka in both records.

Younger middens show somewhat drier floras, especially for a 5.1-ka midden from Cordón de Tuina, with diminished grass abundance and dominance by *Atriplex imbricata* and other prepuna taxa. Slightly wetter conditions may have been present at Cerros de Minta by 4.4 ka, as evidenced by high grass abundance, high species richness and the presence of *Nassella arcuata* as well as numerous summer annuals. High species richness (22 taxa), *N. arcuata* and high grass abundance were also present between 3.4 and 3.3 ka at Pampa Vizcachilla. Species richness dropped to 12 taxa and grass abundance to 23% by 3.2 ka at Pampa Vizcachilla. These drier conditions are also reflected in a 3.2-ka midden from Cerros de Minta, which also has reduced species richness and summer annuals despite local dominance by *Stipa chrysophylla*.

Modern hyperarid floras were established at most sites by 3.0 ka, concomitant with the large sustained drop in grass abundance by 2.8 ka (Fig. 6). Species richness at the higher sites of Cerros de Minta increased between 2.5 and 1.8 ka. This increase preceded a slight rise in grass abundance (to 20–40%) between 1.8 and 1.2 ka at this site as well as at Cordón de Tuina and Pampa Vizcachilla. Three recent middens from Quebrada Chiquinaputo (Table 2) reflect modern hyperarid conditions present slightly downslope from Cerros de Aiquina (Fig. 7). Midden macrofloras indicate a few summer annuals (none occurred at the site today) and several species of prepuna flora, including abundant *Urmenetea atacamensis*, *Cistanthe* spp. and *Atriplex imbricata*. A modern unindurated (still in use or recently abandoned) vizcacha midden collected at Tuina Cave (a few meters from Lejía 386) reveals midden macrofloras almost identical with the list of plants collected within a 500-m radius by C.L. and J.L.B. in two late summer field seasons (Fig. 6 and Table 1).

5.3. Comparison with the low-elevation midden record in the central Atacama

Our midden record from the arid prepuna of the Cordillera Domeyko provides well-dated chronologies of vegetation displacements caused solely by increases in precipitation. As summarized in Table 4, conditions wetter than today occurred at 13.5–9.6 ka (9.5 ka at Cerros de Aiquina), and 7.6–3.2 ka. A short wet interval probably occurred at 1.8–1.2 ka. Increases in summer rainfall were the likely cause for these wet phases due to the abundance of summer annuals and presence of species that today occur further north. Abrupt onset of dry phases (as pronounced as the present hyperarid climate) occurred between 9.6 (9.2) and 8.4 ka and from 3.2 ka to the present. A brief arid event may have occurred at 5.1 ka as evidenced in one midden from Cordón de Tuina.

Among the key issues to address here is whether the timing and extent of the wet and dry phases from our previous midden record along the edge of absolute desert (Latorre et al., 2002) are replicated in the record presented here. Overall agreement between the two records is readily visible when grass abundance values from both records are compared (Fig. 6). Our previous midden record indicated a major wet phase at 13.8–10.5 ka with minor precipitation increases at 7.1–3.5 ka. The wet phase during the late glacial–early Holocene is similar in timing in both records, despite an apparent lag of 1000 years in the higher-elevation record. This lag, however, may be due to the discontinuous nature of the record itself; the lower-elevation record lacked middens dated between 10.2 and 9.5 ka. The higher-elevation record, however, provides much more precise timing for the early Holocene arid phase (see Figs. 7 and 8), which had clearly begun between 9.6 and 9.2 ka (within the 2σ errors of the ^{14}C dates).

A major difference between records during the late glacial was the presence of high tolar shrubs between 13.5 and 12 ka in the higher-elevation record. These taxa were completely absent from coeval lower-elevation middens. The absence of these important taxa at lower elevations could enable us to place upper limits on our precipitation estimates (which in both records are minima) but other factors must be considered. Two reasons could explain this absence: (1) precipitation increases were not sufficient or were too brief to cause these species to migrate far enough downslope; (2) current plant distributions preclude the presence of these taxa in middens from the southern end of the Salar de Atacama. The first explanation is unlikely as taxa found even further up the gradient, such as the steppe grasses *Anatherostipa venusta* and *Nassella nardoides*, were found in the low-elevation record (Latorre et al., 2002). The second explanation seems more likely in this case, as no high tolar species were present on a recent survey across Lomas de Quilvar up to the vicinity of Laguna Miñiques (Fig. 1) (Latorre, 2002).

An important issue is that mid-Holocene increases in precipitation barely recorded at lower elevations are clearly visible in the record presented here, particularly at 7.6–6.3 ka and at 4.5–3.2 ka. Due to a sampling gap, we have yet to resolve the extent of aridity between 6.3 and 4.5 ka, although an arid flora at Cordón de Tuina was present at 5.1 ka. Middens within the prepuna, however, are recording vegetation displacements of 100–350 m in altitude caused by lesser increases in precipitation during parts of the mid-Holocene. One reason why these increases produce only faint traces in the midden floras of lower elevations is that productivity would still have been very low along the absolute desert margin, generating few possibilities for midden formation. For the same reason, the records also differ for the last 3 ka. Whereas lower-elevation middens indicate that the last 3 ka were probably the most arid for the last 22 ka, upper-elevation middens point to a minor wet phase between 1.8 and 1.2 ka. Yet overall, the higher-elevation record not only replicates the major patterns seen in our previous, low-elevation record, but also 'amplifies' precipitation signals that were barely recorded at lower elevations.

5.4. Comparison with other records from the central Atacama

A diverse array of paleoclimate records have recently been developed in the central Atacama region. These include lake and pollen histories from the Chilean Altiplano (Geyh et al., 1999; Grosjean et al., 1995, 2001; Grosjean and Nuñez, 1994; Messerli et al., 1993; Valero-Garcés et al., 1996); archeological records (Nuñez et al., 2001); wetland and groundwater table fluctuations at the base of the Andes (Rech et al., 2001, 2002) and a 100-ka salt core obtained from the deepest portion of the Salar de Atacama (Bobst et al., 2001) (see Fig. 1 for all locations).

Based on a series of different reservoir corrections on radiocarbon dates from lake sediments, Geyh et al. (1999) identified a general wet phase across the Chilean Altiplano between ∼15 and 9 ka. Through the use of a simple hydrologic model, Kull and Grosjean (1998) concluded that precipitation must have doubled to account for lake levels some 25 m higher at Laguna Lejía. Increases in lake levels were accompanied by increases in grass pollen between 11 and 9 ka at Laguna Miscanti (Grosjean et al., 2001) implying expansion of grasslands on the Pacific slope of the Andes. Other evidence for a late glacial wet phase comes from a U-series-dated wet phase between 11.4 and 10.2 ka (Bobst et al., 2001), high groundwater tables between 16 and 9 ka (Rech et al., 2002) and numerous early Archaic sites throughout the central Atacama (Nuñez and Grosjean, 1994; Nuñez et al., 2001). Both our midden records are in agreement with the dating for these wet phases, at 13.8–10.5 ka at lower elevations and at 13.5–9.4 ka at higher elevations; the abundance of summer-flowering annuals and perennials indicates the seasonality of the precipitation. Using the dates reported here for the onset of aridity at 9.6–9.4 ka, lake histories would have lagged 500–600 years behind the rodent middens whereas groundwater fluctuations lagged by approximately 500 years (see also Rech et al., 2003).

There is less agreement about the middle Holocene, which we argue was wetter than today in the central Atacama from both rodent midden and wetland deposits. A case for mid-Holocene aridity has been made based on the presence of gypsum and reduced aquatic pollen in Laguna Miscanti sediments between 9 and 3.9 ka (Grosjean et al., 2001), lower lake levels at Laguna del Negro Francisco (Grosjean et al., 1997b); persistence between 6.8 and 3.2 ka of debris flow-dammed lakes along Quebrada Puripica, a steep canyon that drains the Andean front (Grosjean et al., 1997a); and a hiatus of human occupations between 9 and 3.4 ka known as the *silencio arqueológico* (‘archeological silence’) (Grosjean et al., 1997a; Nuñez et al., 2001).

We feel that most of these indications of mid-Holocene aridity, however, are ambiguous. Although the onset of a dry period at the end of the early Holocene wet phase is well documented at Laguna Miscanti, its duration cannot be determined due to large unsystematic carbon reservoir effects on radiocarbon dates. Furthermore, at ∼27°30′S latitude, Laguna del Negro Francisco is more influenced by the southern westerlies and winter precipitation and lies well beyond the reach of spillover summertime storms from the Altiplano. There is no reason why the climate history at Laguna del Negro Francisco should correlate with that of Laguna Miscanti. At Quebrada Puripica, the purported lake sediments have been reinterpreted as spring deposits by Rech et al. (2003), and correlated with other paleowetland evidence to instead indicate higher groundwater levels in the central and northern Atacama. There is corroborating evidence for a short wet phase dated between 6.2 and 3.5 ka present in the Salar de Atacama core (Bobst et al., 2001). Finally, the beginning of the *silencio arqueológico* surely reflects the onset of hyperaridity in the region, as vegetation retreated upslope and game was restricted to springs and other wetlands. But we feel that the end of the *silencio arqueológico* was determined, not by aridity, but by the slow diffusion of critical technologies from Peru and Bolivia, such as domestication of camelids, and the associated increase in human population.

5.5. *Comparison with other records from the central Andes*

Even larger discrepancies in relative effective moisture arise among records across the central Andes in general. These include cores and shoreline features from Lake Titicaca (Mourguiart et al., 1998; Cross et al., 2000; Baker et al., 2001b) and Salar de Uyuni (Sylvestre et al., 1999; Baker et al., 2001a; Fornari et al., 2001), covered by large and successive paleolakes during the Pleistocene. The late glacial wet phase in the Bolivian Altiplano generally has older dates for the maximum highstands and wet phases. U-series and ^{14}C dating of shoreline tufas in the Uyuni–Coipasa Basin identified two wet phases: one major event between 18.9 and 14.0 ka (Tauca) and a minor event between 10.8 and 9.5 ka (Coipasa), separated by a dry phase (Ticaña) between 14.0 and 10.8 ka (Sylvestre et al., 1999). These highstands are younger than those inferred from a ^{14}C-dated sediment core in the center of the Salar de Uyuni, which indicates successive wet phases throughout the latest Pleistocene, followed by a minor lake stand ∼12.5 ka with no wet phase during the Holocene (Baker et al., 2001a). Lake Titicaca was above present-day levels before 11.5 ka and plummeted to 85 m below present between 8.0 and 5.5 ka as inferred from a core obtained in the deepest portion of the basin (Baker et al., 2001b). Sustained aridity between 6.2 and 2.3 ka has also been inferred from a multiproxy record of hydrologic change at Laguna Taypi Chaka

Kkota, located ~75 km east of Lake Titicaca in the Cordillera Real (Abbott et al., 2000; Wolfe et al., 2001). Onset of aridity occurred here some 3000 years later than at Lake Titicaca and implies that even within the northern Altiplano, sub-regional hydrologic responses at different sites during the late Holocene were complex.

6. Conclusions

This study highlights the value of replicating climatic histories using the same proxy along well-defined environmental gradients. This approach has allowed verification and refinement of paleoclimatic inferences in the central Atacama for the late glacial–early Holocene, though disagreements remain over the nature of mid-Holocene climate among the various researchers working in the Atacama. Some of the discrepancies between paleoclimate records in the central and northern Atacama, the southern Altiplano and the Titicaca Basin may be explained by regional circulation, which is considerably more complex today, and probably in the past, than portrayed by paleoclimatologists. There may be at least two general sources of moisture that contribute to summertime precipitation in the central Andes – air masses over the southern Amazon and the Gran Chaco. These sources may have different forcing and modes of variability, and are not clearly segregated over the region, though the southern Amazon source is dominant in the Lake Titicaca Basin while the Gran Chaco has a greater influence over the southern Altiplano. This could explain why the large paleolakes (e.g. Tauca and Minchin) that probably developed from Lake Titicaca overflow might be decoupled from precipitation in the southern Altiplano and the central and northern Atacama. Furthermore, variability in the moisture sources may or may not be coupled to atmospheric transport from the eastern to western parts of the Altiplano. This transport seems to be modulated by Pacific sea-surface temperature gradients, with increased advection of tropical moisture and more summer rainy days during La Niña than El Niño episodes (Garreaud et al., 2003). This could explain why the Pacific slope of the Andes might be out of phase with Lake Titicaca and other records from the eastern Cordillera. Finally, the effects of regional seasonal insolation variations on these different moisture sources and transport mechanisms are apt to be either weak or very complex. Discrepancies between paleoclimate records suggest that any simple model of climatic change and forcing in the central Andes is probably premature.

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References

Abbott, M., Wolfe, B.B., Aravena, R., Wolfe, A.P., Seltzer, G.O., 2000. Holocene hydrological reconstructions from stable isotopes and paleolimnology, Cordillera Real, Bolivia. Quat. Sci. Rev. 19, 1801–1820.

Aceituno, P., 1988. On the functioning of the southern oscillation in the South American sector. Part I: surface climate. Mon. Weather Rev. 116, 505–524.

Alpers, C.N., Brimhall, G.H., 1988. Middle Miocene climatic change in the Atacama desert, northern Chile: Evidence from supergene mineralization at La Escondida. Geol. Soc. Am. Bull. 100, 1640–1656.

Arroyo, M.T.K., Squeo, F.A., Armesto, J.J., Villagran, C., 1988. Effects of aridity on plant diversity in the northern

Chile Andes: results of a natural experiment. Ann. Missouri Bot. Gard. 75, 55–78.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., Broda, J.P., 2001a. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. Nature 409, 698–701.

Baker, P.A., Rigsby, C.A., Seltzer, G.O., Fritz, S.C., Lowenstein, T.K., Bacher, N.P., Veliz, C., 2001b. The history of South American tropical precipitation for the past 25,000 years. Science 291, 640–643.

Betancourt, J.L., Latorre, C., Rech, J.A., Quade, J., Rylander, K.A., 2000. A 22,000-yr record of monsoonal precipitation from northern Chile's Atacama Desert. Science 289, 1546–1550.

Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), 1990. Packrat Middens: The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson, AZ, 467 pp.

Bobst, A.L., Lowenstein, T.K., Jordan, T.E., Godfrey, L.V., Hein, M.C., Ku, T.-L., Luo, S., 2001. A 106 ka paleoclimate record from drill core of the Salar de Atacama, northern Chile. Palaeogeogr. Palaeoclimatol. Palaeoecol. 173, 21–42.

Borgel, R., 1973. The coastal desert of Chile. In: Amiran, D.H.K., Wilson, A.W. (Eds.), Coastal Deserts, Their Natural and Human Environments. The University of Arizona Press, Tucson, AZ, pp. 111–114.

Caviedes, C., 1973. A climatic profile of the north Chilean desert at latitude 20° south. In: Amiran, D.H.K., Wilson, A.W. (Eds.), Coastal Deserts, Their Natural and Human Environments. The University of Arizona Press, Tucson, AZ, pp. 115–121.

Cross, S.L., Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., 2000. A new estimate of the lowstand level of Lake Titicaca, central Andes, and implications for tropical palaeohydrology. Holocene 10, 21–32.

Fornari, M., Risacher, F., Féraud, G., 2001. Dating of paleolakes in the central Altiplano of Bolivia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 172, 269–282.

Garreaud, R.D., 1999. Multiscale analysis of the summertime precipitation over the central Andes. Mon. Weather Rev. 127, 901–921.

Garreaud, R.D., 2000. Intraseasonal variability of moisture and rainfall over the South American Altiplano. Mon. Weather Rev. 128, 3337–3346.

Garreaud, R.D., Vuille, M., Clement, A., 2003. The climate of the Altiplano: observed current conditions and mechanisms of past changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. S0031-0182(03)00269-4.

Geyh, M.A., Grosjean, M., Núñez, L., Schotterer, U., 1999. Radiocarbon reservoir effect and the timing of the late-Glacial/Early Holocene humid phase in the Atacama desert (northern Chile). Quat. Res. 52, 143–153.

Grimm, E., 1991–1993. Tilia 2.00 Program. Illinois State Museum, Research and Collections Center, Springfield, IL.

Grosjean, M., 1994. Paleohydrology of the Laguna Lejía (north Chilean Altiplano) and climatic implications for late-glacial times. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109, 89–100.

Grosjean, M., 2001. Mid-Holocene climate in the south-central Andes: humid or dry? Reply. Science 292, 2391a.

Grosjean, M., Nuñez, L.A., 1994. Lateglacial, Early and Middle Holocene environments, human occupation, and resource use in the Atacama (Northern Chile). Geoarchaeology 9, 271–286.

Grosjean, M., Geyh, M.A., Messerli, B., Schotterer, U., 1995. Late-glacial and early Holocene lake sediments, groundwater formation and climate in the Atacama Altiplano 22°–24°S. J. Paleolimnol. 14, 241–252.

Grosjean, M., Nuñez, L., Cartajena, I., Messerli, B., 1997a. Mid-Holocene climate and culture change in the Atacama Desert, northern Chile. Quat. Res. 48, 239–246.

Grosjean, M., Valero-Garcés, B.L., Geyh, M.A., Messerli, B., Schotterer, U., Schreier, H., Kelts, K., 1997b. Mid and late Holocene limnogeology of the Laguna del Negro Francisco, northern Chile, and its palaeoclimatic implications. Holocene 7, 151–159.

Grosjean, M., van Leeuwen, J.F.N., van der Knaap, W.O., Geyh, M.A., Ammann, B., Tanner, W., Messerli, B., Núñez, L.A., Valero-Garcés, B.L., Veit, H., 2001. A 22,000 ^{14}C year BP sediment and pollen record of climate change from Laguna Miscanti (23°S), northern Chile. Global Planet. Change 28, 35–51.

Holmgren, C., Betancourt, J.L., Rylander, K.A., Roque, J., Tovar, O., Zeballos, H., Linares, E., Quade, J., 2001. Holocene vegetation history from fossil rodent middens near Arequipa, Peru. Quat. Res. 56, 242–251.

Kull, C.M., Grosjean, M., 1998. Albedo changes, Milankovitch forcing, and late Quaternary climate changes in the central Andes. Clim. Dyn. 14, 871–881.

Latorre, C., 2002. Clima y vegetación del Desierto de Atacama durante el Cuaternario tardío, II Región, Chile. PhD Thesis, Universidad de Chile, Santiago, 173 pp.+xii.

Latorre, C., Betancourt, J.L., Rylander, K.A., Quade, J., 2002. Vegetation invasions into Absolute Desert: A 45,000-yr rodent midden record from the Calama-Salar de Atacama Basins, northern Chile (22–24°S). Geol. Soc. Am. Bull. 114, 349–366.

Lenters, J.D., Cook, K.H., 1995. Simulation and diagnosis of the regional summertime precipitation climatology of South America. J. Clim. 8, 2988–3005.

Lenters, J.D., Cook, K.H., 1997. On the origin of the Bolivian high and related circulation features of the South American climate. J. Atmos. Sci. 54, 656–677.

Marinovic, N., Lahsen, A., 1984. Geología de la Hoja Calama, Región de Antofagasta. Carta Geológica de Chile, Escala 1:250.000, 58. Servicio Nacional de Geología y Minería, Santiago de Chile, 140 pp.

Marticorena, C., Matthei, O., Rodriguez, R., Kalin Arroyo, M.T., Muñoz, M., Squeo, F., Arancio, G., 1998. Catalogo de la flora vascular de la Segunda Región (Región de Antofagasta), Chile. Gayana Bot. 55, 23–83.

Matthei, O.R., 1965. Estudio crítico de las gramíneas del Género *Stipa* en Chile. Gayana Bot. 13, 2–137.

Meserve, P.L., Glanz, W.E., 1978. Geographical ecology of small mammals in the northern Chilean arid zone. J. Biogeogr. 5, 135–148.

Messerli, B., Bonani, G., Burgi, A., Geyh, M.A., Graf, K., Grosjean, M., Ramseyer, K., Romero, H., Schotterer, U., Schreier, H., Vuille, M., 1993. Climate change and natural resource dynamics of the Atacama Altiplano during the last 18,000 years. A preliminary synthesis. Mt. Res. Dev. 13, 117–127.

Mortimer, C., 1980. Drainage evolution in the Atacama Desert of northernmost Chile. Rev. Geol. Chile 11, 3–28.

Mourguiart, P., Correge, T., Wirrmann, D., Argollo, J., Montenegro, M.E., Pourchet, M., Carbonel, P., 1998. Holocene palaeohydrology of Lake Titicaca estimated from an ostracod-based transfer function. Palaeogeogr. Palaeoclimatol. Palaeoecol. 143, 51–72.

Nuñez, L., Grosjean, M., 1994. Cambios ambientales pleistoceno-holocénicos: Ocupación humana en la Puna de Atacama (Norte de Chile). Estud. Atacameños 11, 11–24.

Nuñez, L., Grosjean, M., Cartajena, I., 2001. Human dimensions of late Pleistocene/early Holocene arid events in southern South America. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, New York, pp. 105–117.

Pearson, O.P., 1948. Life history of mountain viscachas in Peru. J. Mammal. 29, 345–374.

Pearson, O.P., Ralph, C.P., 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Mem. Mus. Hist. Nat. 'Javier Prado' 18, 5–80.

Pizzimenti, J.J., De Salle, R., 1980. Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. Biol. J. Linn. Soc. 13, 263–285.

Placzek, C., Quade, J., Betancourt, J.L., 2001. Holocene lake level fluctuations of Lago Aricota, southern Peru. Quat. Res. 56, 181–190.

Quade, J., Rech, J., Betancourt, J., Latorre, C., 2001. Mid-Holocene climate in the south-central Andes: humid or dry? Response. Science 292, 2391a.

Rech, J., Quade, J., Betancourt, J.L., 2001. Paleoclimatic reconstruction of the Atacama Desert (18–26°S): Evidence from wetland deposits. Proceedings from the Central Andean Paleoclimate Workshop, Tucson, AZ.

Rech, J., Quade, J., Betancourt, J.L., 2002. Late Quaternary paleohydrology of the central Atacama Desert (22–24°S), Chile. Geol. Soc. Am. Bull. 114, 334–348.

Rech, J., Pigati, J.S., Quade, J., Betancourt, J.L., 2003. Re-evaluation of mid-Holocene wetland deposits at Quebrada Puripica, northern Chile. Palaeogeogr. Palaeoclimatol. Palaeoecol. S0031-0182(03)00278-5.

Rojas, F., 1994. Revisión de las especies de la Tribu Stipae (Poaceae) en Bolivia. Tesis de Magister, Universidad de Concepción, Concepción, 157 pp.

Rundel, P.W., Dillon, M.O., Palma, B., 1996. Flora and vegetation of Pan de Azucar National Park in the Atacama Desert of northern Chile. Gayana Bot. 53, 295–315.

Rundel, P.W., Dillon, M.O., Palma, B., Mooney, H.A., Gulmon, S.L., Ehleringer, J.R., 1991. The phytogeography and ecology of the Coastal Atacama and Peruvian Deserts. Aliso 13, 1–49.

Seltzer, G.O., Baker, P., Cross, S., Dunbar, R., Fritz, S., 1998. High-resolution seismic reflection profiles from Lake Titicaca, Peru-Boliva: evidence for Holocene aridity in the tropical Andes. Geology 26, 167–170.

Stoertz, G.E., Ericksen, G.E., 1974. Geology of salars in northern Chile. Geol. Surv. Prof. Pap. 811, 1–65.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.

Sylvestre, F., Servant, M., Servant-Vildary, S., Causse, C., Fournier, M., Ybert, J.-P., 1999. Lake-level chronology on the Southern Bolivian Altiplano (18°–23°S) during late-glacial time and the early Holocene. Quat. Res. 51, 54–66.

Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.-N., Mikhalenko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice cores. Science 282, 1858–1864.

Valero-Garcés, B.L., Grosjean, M., Schwalb, A., Geyh, M., Messerli, B., Kelts, K., 1996. Limnogeology of Laguna Miscanti: evidence for mid to late Holocene moisture changes in the Atacama Altiplano (Northern Chile). J. Paleolimnol. 16, 1–21.

Villagrán, C., Armesto, J.J., Kalin Arroyo, M.T., 1981. Vegetation in a high Andean transect between Turi and Cerro León in Northern Chile. Vegetatio 48, 3–16.

Villagrán, C., Arroyo, M.T.K., Marticorena, C., 1983. Efectos de la desertización en la distribución de la flora andina de Chile. Rev. Chil. Hist. Nat. 56, 137–157.

Vuille, M., 1999. Atmospheric circulation over the Bolivian Altiplano during dry and wet periods and extreme phases of the Southern Oscillation. Int. J. Climatol. 19, 1579–1600.

Wolfe, B.B., Aravena, R., Abbott, M.B., Seltzer, G.O., Gibson, J.J., 2001. Reconstruction of paleohydrology and paleohumidity from oxygen isotope records in the Bolivian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 176, 177–192.

Zhou, J., Lau, K.-M., 1998. Does a monsoon climate exist over South America? J. Clim. 11, 1020–1040.