

Pollen analyses from a 50 000-yr rodent midden series in the southern Atacama Desert (25° 30' S)

ANTONIO MALDONADO,¹ JULIO L. BETANCOURT,^{2*} CLAUDIO LATORRE³ and CAROLINA VILLAGRAN⁴

¹ Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Departamento de Biología, Facultad de Ciencias, Universidad de La Serena, La Serena, Chile

² Desert Laboratory, US Geological Survey and University of Arizona, 1675 W. Anklam Rd, Tucson, AZ 85745, USA

³ CASEB-Departamento de Ecología, P. Universidad Católica de Chile, Alameda 340, Santiago, Chile

⁴ Laboratorio de Sistemática y Ecología Vegetal, Departamento de Ciencias Ecológicas, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile

Maldonado, A., Betancourt, J. L., Latorre, C. and Villagran, C. 2005. Pollen analyses from a 50 000-yr rodent midden series in the southern Atacama Desert (25° 30' S). *J. Quaternary Sci.*, Vol. 20 pp. 493–507. ISSN 0267-8179.

Received 1 November 2004; Revised 1 April 2005; Accepted 6 April 2005

ABSTRACT: Precipitation in northern Chile is controlled by two great wind belts—the southern westerlies over the southern Atacama and points south (>24° S) and the tropical easterlies over the northern and central Atacama Desert (16–24° S). At the intersection of these summer and winter rainfall regimes, respectively, is a Mars-like landscape consisting of expansive surfaces devoid of vegetation (i.e. absolute desert) except in canyons that originate high enough to experience runoff once every few years. Pollen assemblages from 39 fossil rodent middens in one of these canyons, Quebrada del Chaco (25° 30' S), were used to infer the history of vegetation and precipitation at three elevations (2670–2800 m; 3100–3200 m; 3450–3500 m) over the past 50 000 years. When compared to modern conditions and fossil records to the north and south, the pollen evidence indicates more winter precipitation at >52, 40–33, 24–17 k cal. yr BP, more precipitation in both seasons at 17–14 k cal. yr BP, and more summer precipitation from 14–11 k cal. yr BP. Younger middens are scarce at Quebrada del Chaco, and the few Holocene samples indicate hyperarid conditions comparable to today. The only exception is a pollen assemblage that indicates a brief but significant interlude of increased winter precipitation in the last millennium. Copyright © 2005 John Wiley & Sons, Ltd.



KEYWORDS: fossil rodent middens; pollen; southern westerlies; tropical easterlies; absolute desert; Atacama Desert; northern Chile

Introduction

In Chile, large-scale patterns in plant biogeography are determined largely by the interface between two large climatic systems that control seasonal precipitation patterns across South America. The southern westerlies bring Pacific moisture to central and southern Chile. Their northernmost influence is manifest in low-pressure troughs or cut-off lows that allow penetration of winter storms into the southern Atacama Desert (24–26° S), and occasionally as far north as 18° S (Montecinos *et al.*, 2000; Rutllant and Fuenzalida, 1991; Vuille and Ammann, 1997). In contrast, the tropical easterlies and associated summer monsoon govern precipitation patterns over tropical and subtropical South America. The South American Summer Monsoon extends from the Amazon Basin and Gran Chaco lowlands southwest and west over the Bolivian Altiplano, spilling over the Pacific slope of the Andes onto

the upper elevations of the northern and central Atacama (Garreaud and Aceituno, 2002). On annual timescales, features of both wind systems are modulated, usually in opposite phase, by the El Niño–Southern Oscillation (ENSO). During El Niño (La Niña) years the subtropical jet and westerlies tend to strengthen (weaken) over central Chile, enhancing (reducing) northward penetration of winter storms, while the summer easterlies weaken (strengthen) and reduce (increase) the number of precipitation days over the Bolivian Altiplano (Garreaud *et al.*, 2003; Vuille and Keimig 2004). Similar antiphasing remains to be identified on longer timescales.

The Central Andes, with mean elevations exceeding 5000 m, impose significant rainshadows on both westerly and easterly air masses that contribute to the aridity in the Monte Desert of Argentina and the Atacama Desert of northern Chile, respectively. The intersection of the tropical easterlies and southern westerlies with the orographic effect of the Andes results in a major climatic and biogeographic boundary, the so-called 'Arid Diagonal of South America', which extends from south-eastern Argentina to northwestern Peru (Garleff *et al.*, 1991; Villagrán and Hinojosa, 1997).

Modern biogeographic patterns and limited fossil evidence suggest that the general location of the Arid Diagonal has been

*Correspondence to: Julio L. Betancourt, Desert Laboratory, US Geological Survey, University of Arizona 1675 W. Anklam Road, Tucson, AZ 85745, USA. E-mail: jlbetanc@usgs.gov

relatively stable over the Neogene (Villagrán and Hinojosa, 1997). This does not rule out, however, important fluctuations in Quaternary climate that could have displaced plant and animal distributions up to several hundred metres in elevation or hundreds of kilometres in latitude. Such fluctuations along the Arid Diagonal, if properly documented, could contribute important insights about long-term variability in the strengths and phasing of the southern westerlies and tropical easterlies.

The pace of Quaternary studies in the Central Andes has accelerated in the past decade, though little consensus has been reached on the exact timing and causes for changes in the strengths of the southern westerlies or tropical easterlies, much less on their relative phasing. One controversy centres on whether, during the Last Glacial Maximum (24–16 k cal. yr BP), the southern westerlies shifted equatorward (Heusser, 1989; Heusser *et al.*, 1996; Veit 1996; Moreno *et al.*, 1999; Lamy *et al.*, 1998, 1999) or intensified and focused year round south of 41° S (Markgraf *et al.*, 1992; Wyrwoll *et al.*, 2000). Another debate focuses on the chronology of palaeolake highstands and lowstands on the Bolivian Altiplano during the full to late Glacial and their relationship to millennial-scale variability in the strength of the tropical easterlies. Depending on author, proxy type and region, inferences about the timing for maximum summer wetness in the Central Andes shifts from 26–14.5 k cal. yr BP (Baker *et al.*, 2001; Fritz *et al.*, 2004) to 19–12 k cal. yr BP (Clapperton *et al.*, 1997; Sylvestre *et al.*, 1999; Argollo and Mourguiart 2000; Fornari *et al.*, 2001) on the Bolivian Altiplano, and from 26–16 k cal. yr BP (Bobst *et al.*, 2001) to 16–10.5 k cal. yr BP in the Atacama region (22–24° S)

(Betancourt *et al.*, 2000; Grosjean *et al.*, 2001; Latorre *et al.*, 2002; Rech *et al.*, 2002). Depending on chronology, at least one permutation of pluvial conditions across the Arid Diagonal could be interpreted as an in-phase strengthening of the southern westerlies and tropical easterlies. At stake is the ability to sort out the influences of seasonal insolation variations on the strength of the Bolivian High (an upper level [~ 200 mb] anticyclone that develops during summer over the Bolivian Altiplano) and monsoonal intensity, as well as on tropical Pacific sea surface temperature (SST) gradients that today control the frequencies and maximum extent of both summer and winter storms in the central Andes (10–30° S).

The central (22–24° S) and southern (24–26° S) Atacama Desert of northern Chile boast a steep climatic gradient across latitude and elevation that spans summer and winter-dominant rainfall regimes (Fig. 1), and thus comprise an ideal setting for investigating the interplay between the tropical easterlies and southern westerlies. In this hyperarid, mountainous environment, vegetation displacements with elevation can be inferred from pollen and plant macrofossil assemblages in fossil rodent middens (Betancourt and Saavedra 2002; Betancourt *et al.*, 2000; Latorre *et al.*, 2002, 2003) to reconstruct changes in the seasonality and abundance of precipitation. Growing season temperatures in this cold desert are rather mild, so that summer heat load plays a negligible role in plant water relations. Unlike in warmer deserts of the world, the lower limits of plants in the Atacama are instead governed exclusively by seasonal precipitation amounts. Summer precipitation is convective, is generally determined by the number of precipitation

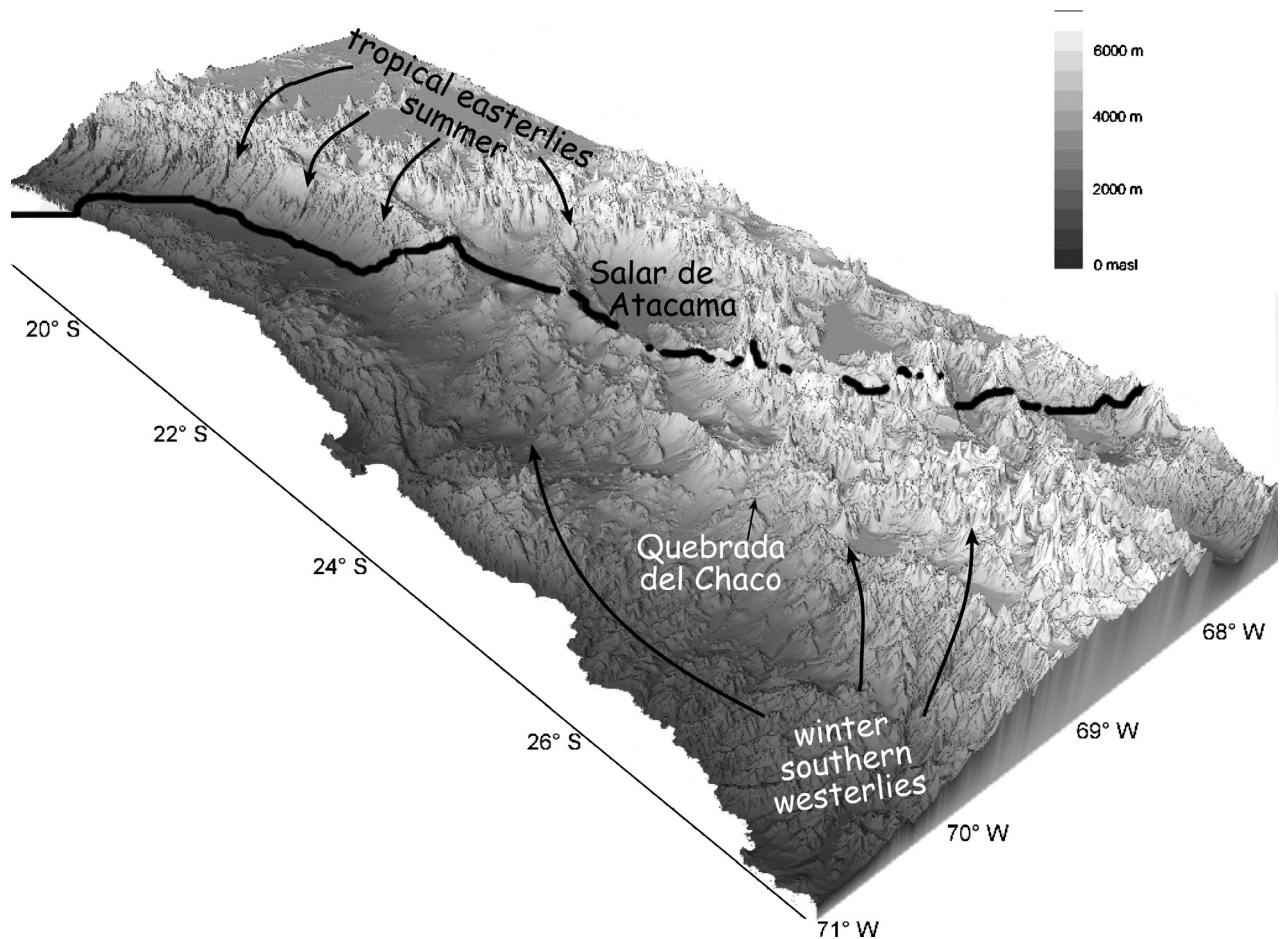


Figure 1 Three-dimensional map of the Atacama region showing latitudinal–elevational boundary (diagonal line) between summer-dominant rainfall regime to the northeast and winter-dominant rainfall regime to the southwest. The boundary was adapted from Houston and Hartley (2003). Locations of Salar de Atacama and Quebrada del Chaco are indicated

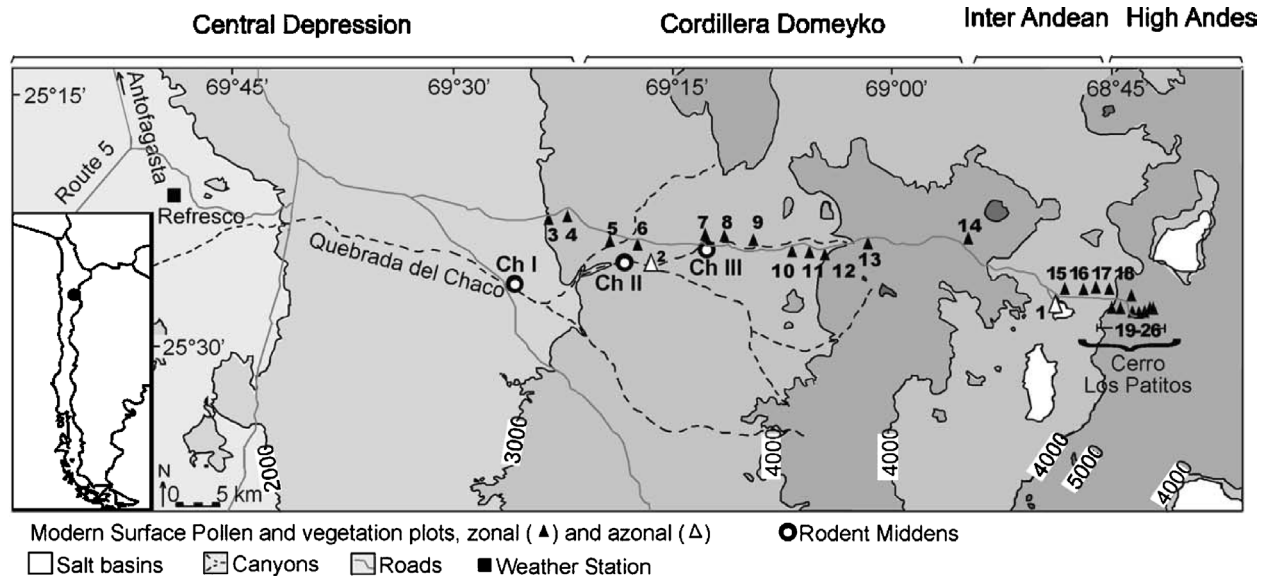


Figure 2 Map of the study area showing location of fossil midden locations (circles Chaco I (ChI), Chaco II (ChII) and Chaco III (ChIII)); modern surface pollen sites (open triangles 1 and 2 are for the wetland sites; closed triangles 3–26 are for other sites). White areas correspond to salts basins and the closed square indicates the closest meteorological station (Refresco)

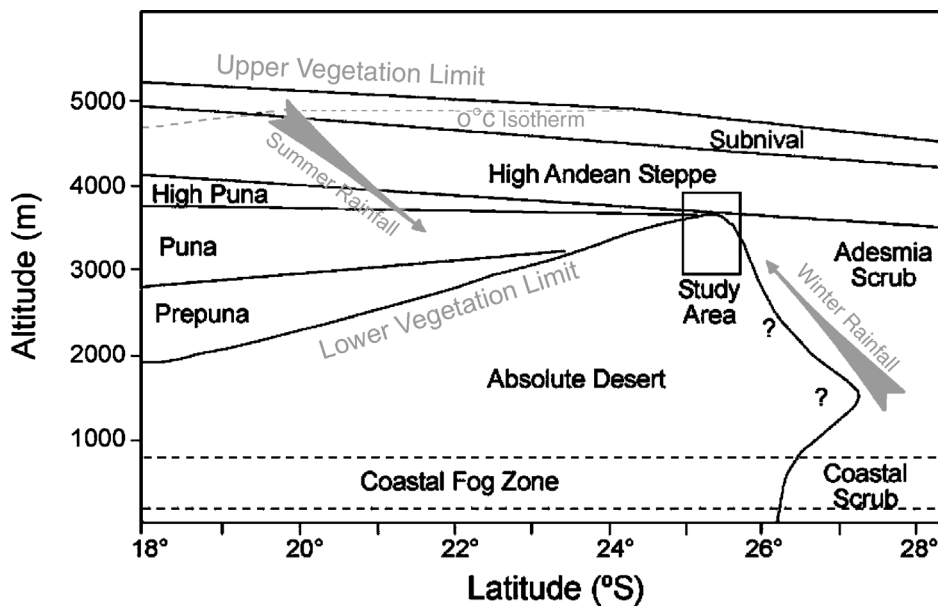


Figure 3 Latitude/elevation distribution of vegetation zones and absolute desert in the Atacama region (modified from Schmithusen (1956))

days (Vuille and Keimig 2004), rains out quickly at the highest elevations as storm cells move in from east to west and descend the Pacific slope of the Andes, and is thus confined to the highest (>3000 m) and easternmost elevations. Winter precipitation is mostly advective, decreases from southwest to northeast, and is generally not subject to orographic effects (does not vary systematically with elevation). In the southern Atacama (24–26° S), these circumstances are ideal for sorting out the influence of seasonal precipitation changes on past vegetation displacements. At its simplest, displacements observed only at the highest elevations can be attributed to summer convective precipitation due to stronger tropical easterlies, whereas those registered at all elevations can be attributed to winter advective rainfall with northward expansion of the southern westerlies.

Here, we report on a vegetation history from pollen preserved in three series of fossil rodent middens (Betancourt

and Saavedra, 2002) at three elevations (2670–2800 m, 3100–3200 and 3450–3500 m) in Quebrada del Chaco (25° 30' S; 69° 15' W, Fig. 2), a shallow canyon originating in the Cordillera de Domeyko that forms the headwaters of the Rio Taltal. Analysis of plant macrofossils in the middens, as well as the alluvial stratigraphic history of Quebrada del Chaco, will be presented elsewhere. The study area lies near the midpoint of the Arid Diagonal, precisely at the latitude (25.30° S) where absolute desert (defined as relatively continuous stretches of land beyond the dry limits of vascular plants) penetrates to its highest elevation in the southern Atacama Desert (Fig. 3). This sector defines the hinge point for biogeographic assemblages adapted to summer versus winter rains (Arroyo *et al.*, 1988; Moreno *et al.*, 1994; Villagrán *et al.*, 1983), and arguably supports the lowest biodiversity, as well as lowest vegetation cover and heterogeneity, in the Americas. In this unique

hyperarid environment, we compare and contrast pollen assemblage changes across the three elevations to discriminate the seasonality and source of inferred increases in precipitation at discrete times of midden deposition over the last 50 000 years. We conclude by acknowledging agreements and reconciling differences between our inferences and other palaeoclimatic evidence in the region.

Physical and ecological setting

Quebrada del Chaco (22° 30' S; 69° 15' W, Fig. 2) is a long and narrow, dry river canyon that originates at ~5000 m in the western slopes of the Cordillera de Domeyko (locally referred to as the Cordillera Taltal). The 50-km west-flowing canyon spans elevations from ~4000 down to 1500 m, where it empties into the longitudinal valley that separates the Cordillera de Domeyko from the coastal mountains. Quebrada del Chaco is very close to the maximum inland penetration of absolute desert, which extends up to 4000 m across expansive interfluvies. Sparse Andean vegetation grows primarily above 3100 m in the bottom of the main canyon and its tributaries. Below 3100 m, there is only an occasional plant along the canyon's thalweg, though occasional wet winters can produce patches of annuals in the floodplain down to 2500 m. Rodent middens were collected from rock outcrops within the main canyon in three elevational bands (2670–2800 m; 3100–3200 m; 3450–3500 m).

There are no weather stations nearby, and mean annual precipitation tends to increase abruptly to the north and south where stations are located. Potrerillos (some 100 km to the south at 26° 30' S; 69° 27' W; 2850 m) receives 52.2 mm yr⁻¹, while Refresco (25° 19' S; 69° 52' W; 1850 m; Fig. 2) gets 9.2 mm yr⁻¹ (Hajek and di Castri, 1975). Much of this scant rainfall originates in winter and may be due to occasional cut-off lows from more southerly polar fronts advecting moist air masses into the region (Vuille and Ammann, 1997). Winter precipitation in this region of Chile varies with prevailing winds and exposure, and not with elevation (Houston and Hartley, 2003). At the highest elevations (above 4000 m), however, most of the winter precipitation falls as snow and is largely lost to sublimation before it can infiltrate the soil and become available to plants (Vuille and Ammann, 1997). At the latitude of Quebrada del Chaco, some convective rainfall of tropical origin can occur in late summer, as observed by the authors for the Cordillera de Domeyko on April 1, 2000, and again in late February 2001. Rainout occurs abruptly as these air masses descend the west slope of the Andes, and any summer precipitation is generally confined to the uppermost elevations (>3500 m) (Arroyo et al. 1998). We note that Quebrada del Chaco is separated from the crest of the Andes by a 30-km stretch of Chilean Altiplano that averages ~4000 m elevation and the Cordillera Domeyko, which exceeds 5000 m and imposes a secondary rainshadow on convective thunderstorms from the east.

The flora of Quebrada del Chaco and the adjacent region is extremely depauperate. A recent survey recorded just 55 taxa of vascular plants along two different elevational transects in the Cordillera de Domeyko and the adjacent Andes (Latorre, 2002). This contrasts with a richer flora of ~90 taxa at Lullail-laco National Park (24° 30'–25° 10' S, Arroyo et al., 1998) and 144 taxa recorded along comparable transects at 26° S (Arroyo et al., 1988; Moreno et al., 1994). The vegetation belts (puna and prepuna) characteristic of mid-elevations in northern and central Atacama are mostly missing (Fig. 3), generally restricted

to small gullies and ravines. Only above 4000 m does sparse vegetation (total cover less than 5%) actually cover hillslopes or the expansive 'pampas' (flatlands) that characterise the Atacama Desert and Chilean Altiplano (Fig. 4). Throughout this report, we refer to hillslope or 'pampa' vegetation as zonal, and riparian or wetland vegetation as azonal.

As a baseline for our palaeoecological interpretations, we surveyed plant community composition and cover along an elevational transect from the Andes proper to Quebrada del Chaco (Fig. 2). Nomenclature used here follows Marticorena et al. (1998). We found that the upper limit of vascular plants lies at ~4500 m followed by two vegetation belts that we classify here as subnival (4300–4500 m) and Andean (4100–4300 m) (Fig. 4). In these two zones, plant cover never exceeds 10%, is generally less than 5% and in some plots approximates 0% cover (Fig. 4). The subnival belt is relatively rich in species despite the low cover values. Species in the upper subnival belt (>4450 m) include perennial herbs and sub-shrubs such as *Menonvillea virens* (Brassicaceae), *Perezia atacamensis* (Asteraceae) and *Mulinum crassifolium* (Apiaceae). The lower subnival (4375–4325 m) includes the diminutive herbs *Chaetanthera revoluta* and *C. sphaeroidalis* (Asteraceae), *Lenzia chamaepitys* (Portulacaceae), *Urbania pappigera* (Verbenaceae) and the steppe grass *Stipa frigida* (Poaceae). Higher plant cover values, mostly due to *Stipa frigida* (2–5%), characterise the Andean belt.

From 4150 to 3850 m, the flanks of the Cordillera de Domeyko are almost completely dominated by *Stipa frigida*, whereas between 3850 and 3450 m vegetation is mostly restricted to dry watercourses. The latter pattern conforms to an extreme version of what Monod (1954) described as 'contracted vegetation' in the Saharan and Arabian deserts, where plant growth is limited to *wadis* and depressions that concentrate and channel rainfall. Fragmented puna belt vegetation in the canyon bottom of Quebrada del Chaco includes *Junellia bryoides* (Verbenaceae), *Adesmia cf. hystrix* (Fabaceae), *Ephedra breana* (Ephedraceae), and *Stipa frigida*. Other species that appear along small washes are *Cristaria andicola* (Malvaceae) and occasional patches of *Stipa frigida*, primarily on protected, south-facing slopes. Isolated, perennial plants along the washes become scarce between 3450 and 2670 m and mostly disappear below 2600 m. During wet winters, xerophytic annuals (*Nolana*, *Phacelia*, *Cistanthe*) appear down to 2500 in the floodplain of Quebrada del Chaco.

Several washes and pools appear within Quebrada del Chaco (i.e. Vegas del Chaco: 3375 m) and at Salar de la Azufrera (3500 m). The vegetation associated with these small semi-permanent supplies of water is characterised by *Acaena magellanica* (Rosaceae), *Lycium humile* (Solanaceae), *Atriplex madariagae* (Chenopodiaceae) and several species of Juncaceae and Poaceae.

Methods

We analysed pollen from 37 fossil rodent middens collected from three different elevations within Quebrada del Chaco (Fig. 2, Table 1): Chaco I (14 middens, 2670–2800 m); Chaco II (6 middens, 3100–3200 m); and Chaco III (17 middens, 3450–3500 m). The three Quebrada del Chaco midden chronologies represent discrete temporal snapshots comprising individual middens from different sites in the same general area (elevation), usually within a 1–2 km radius. Except in a few cases (Field No. 509A–D, Table 1), there is no stratigraphic continuity in the midden chronologies. Faecal pellets from each

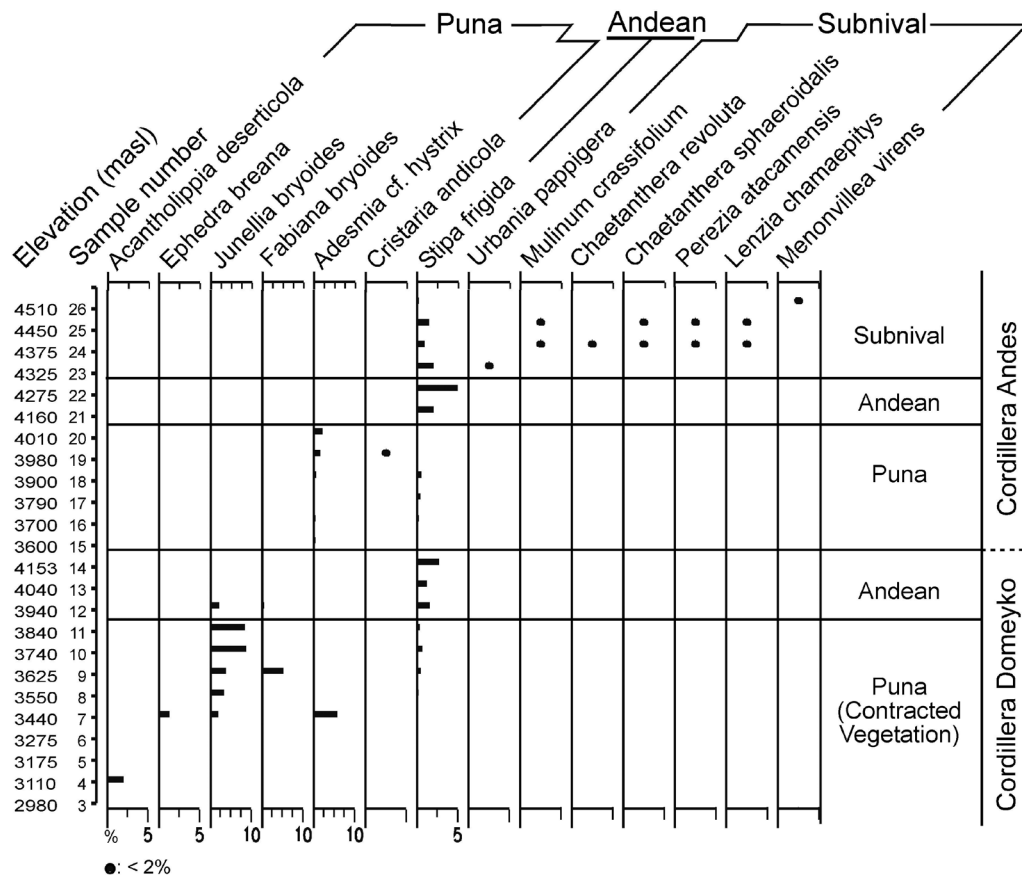


Figure 4 Elevational distribution of plant cover in east-west transect across the Andes, Cordillera Domeyko and Quebrada del Chaco. Black circles represent taxa with percentage < 2%

midden were ¹⁴C-dated at the NSF–University of Arizona Accelerator Facility and calibrated to calendar years using Calib 4.3 (Intcal 98 calibration curve; Stuiver *et al.*, 1998). All ages reported here for middens ≤ 20 000 ¹⁴C yr BP were converted to calendar years, using the mean for plotting purposes. For older middens, we plotted actual ¹⁴C ages (Table 1).

Middens were processed following procedures described in Betancourt *et al.* (2001). Pollen from both modern soil samples (see below) and fossil midden matrix were extracted using standard techniques (Faegri and Iversen, 1989). The pollen sum for each sample included a minimum of 300 grains. Pollen zones were determined using CONISS (constrained incremental sum of squares) cluster analysis (Grimm, 1987), and the relationships between fossil midden and modern surface pollen assemblages were expressed in the form of dendrograms and Euclidean distances.

Surface sediment was collected to characterise the modern pollen rain at a total of 26 stations along our elevational plant transects (Fig. 2) within the Precordillera (stations 3–11), Cordillera de Domeyko (12–14) and High Andes (15–26). Pollen samples were also collected from small bogs around local springs surrounded by absolute desert (stations 1–2). We have not investigated the time interval represented by a single surface sample in this hyperarid and windy environment, and we do not reconcile potential differences between surface soils and wetland sediments. Pollen was not recovered from samples between 2980 and 3175 m (stations 3–5). This suggests that the regional pollen rain, which is carried aloft by wind, is mostly negligible. This lack of pollen in surface sediments at lower elevations would also indicate that there is relatively little reworking of old sediments containing pollen through deflation. Our best guess is that the Quebrada del Chaco sur-

face pollen samples each represent the last few months or at most a few years of pollen deposition.

On the pollen signal in rodent middens

Unlike for North American woodrat (*Neotoma* spp.) middens (King and Van Devender, 1977; Thompson, 1985; Davis and Anderson, 1987, 1988; Van Devender, 1988; Anderson and Van Devender 1991; Betancourt *et al.*, 2001), there have been no studies in the Atacama Desert that suggest how pollen becomes incorporated into rodent middens. Several authors have discussed how pollen accumulates in North American woodrat middens, and what the pollen might actually represent. Whereas some argue that midden pollen faithfully represents regional vegetation (King and Van Devender, 1977), others suggest that it chiefly represents local vegetation while also incorporating regional pollen rain (Davis and Anderson, 1987; Anderson and Van Devender, 1991 Thompson, 1985).

Several processes may be involved in the deposition of pollen in a rodent midden, including (a) pollen transported by wind, or carried in on (b) the animal's fur or (c) on the plants it drags into its den. Pollen abundances in middens are affected not only by local plant cover, but also by the dietary selectivity of the animal and the relative importance of high-pollen producing wind-pollinated (anemophilous) species versus low-pollen producing ones that are insect- or animal-pollinated (entomophilous or zoophilous). We note that midden-forming rodents in the Atacama Desert (*Phyllotis*, *Lagidium* and *Abrocoma*) can ill afford to be choosy, and therefore should be considered generalists (see discussion in Betancourt and Saavedra,

Table 1 Locality information and radiocarbon dates for the 37 middens used in this study

Pollen sample	Field no.	Latitude	Longitude	Elev. (m)	Aspect	Rock type	¹⁴ C Lab. No.	¹⁴ C date (yr BP)	St. dev.	δ ¹³ C	Calibrated age ^a (cal. yr BP)	Mid-point ^b
2600–2900 m												
1	527	25°27.621'	69°24.709'	2800	SW	ignimbrite	GX26848	610	100	–23.1	620,608,554	587
2	513	25°27.414	69°25.176'	2800	SW	ignimbrite	GX26833	880	70	–22.8	756,753,740	798
3	517	25°26.183'	69°27.070'	2670	S	limestone	GX26819	940	60	–22.4	884,867,826, 813,793	832
5	526B	25°27.623'	69°24.898'	2860	SW	ignimbrite	GX26827	13030	340	–24.5	15638	15312
6	509C	25°26.183'	69°27.070'	2670	S	limestone	GX26672	15120	560	–23	18051	18059
7	519	25°26.183'	69°27.070'	2670	S	limestone	GX26820	17070	290	–23.6	20295	20298
8	509B	25°26.183'	69°27.070'	2670	S	limestone	GX26671	19400	770	–23.1	22976	22988
9	512	25°26.188'	69°27.104'	2670	S	limestone	GX26832	20110	340	–24.5	23793	23780
11	518	25°26.183'	69°27.070'	2670	S	limestone	GX26826	>33800	—	–21.5	—	—
12	508	25°26.183'	69°27.070'	2670	S	limestone	GX26670	>36350	—	–22.2	—	—
13	509D	25°26.183'	69°27.070'	2670	S	limestone	GX26673	>38880	—	–23.1	—	—
14	509A1	25°26.183'	69°27.070'	2670	S	limestone	GX26675	>52200	—	–22.3	—	—
15	516A	25°26.183'	69°27.070'	2670	S	limestone	GX26674	>52200	—	–22.3	—	—
16	516B	25°26.183'	69°27.070'	2670	S	limestone	GX26676	>52200	—	21.3	—	—
3100–3200 m												
17	528B	25°25.433'	69°17.550'	3200	SE	limestone	GX26830	1270	100	–23.9	1172	1172
18	528A	25°25.433'	69°17.550'	3200	SE	limestone	GX27163	1470	120	–23.7	1329,1319,1314	1389
19	507D	25°25.774'	69°19.025'	3100	N	breccia	GX27166	1620	60	–20.9	1518	1477
20	533	25°25.774'	69°19.025'	3100	N	breccia	GX26821	2590	70	–20.4	2739	2630
21	507A	25°25.774'	69°19.025'	3100	N	breccia	GX26816	4530	80	–20.9	5279,5166,5131, 5106,5070	5145
22	507C	25°25.774'	69°19.025'	3100	N	breccia	GX26818	7630	90	–18.4	8391	8397
3450–3500 m												
23	515B	25°24.649'	69°17.341'	3470	N	ignimbrite	GX27167	550	60	–24.2	536	566
24	497B	25°24.537'	69°12.255'	3500	N	ignimbrite	GX26824	800	80	–24.4	686	708
25	495A	25°24.222'	69°13.165'	3450	SE	ignimbrite	GX26822	940	60	–22.4	884,867,826, 813,793	832
26	503A	25°24.764'	69°13.066'	3460	N	ignimbrite	GX26840	4550	80	–23.5	5287,5156, 5143,5099,5089	5178
27	495B	25°24.222'	69°13.165'	3450	SE	ignimbrite	GX26839	9010	330	–23.2	10186	10050
29	504	25°24.742'	69°12.695	3460	N	ignimbrite	GX26831	10010	70	–22.4	1534,11524, 11338,11316,1130	11440
30	496	25°24.537'	69°12.255'	3500	N	ignimbrite	GX26847	10310	260	–24.3	12100,12004,11976	12072
32	499B	25°24.778'	69°13.002'	3470	N	ignimbrite	GX26815	10660	140	–23.9	12812,12719,12665	12639
33	498A	25°24.778'	69°13.002'	3470	N	ignimbrite	GX27168	11300	170	–23.4	13173	13238
34	511A	25°24.739'	69°12.742'	3450	N	ignimbrite	GX26817	12640	640	–24	15250,14584,14467	14913
35	500A	25°24.633'	69°12.421	3450	N	ignimbrite	GX26828	12730	350	–24.7	15348	15025
36	500C	25°24.633'	69°12.421	3450	N	ignimbrite	GX26843	12810	390	–24.8	15426	15105
37	515A	25°24.649'	69°17.341'	3470	N	ignimbrite	GX27164	12870	140	–24.9	15482	15252
38	498B	25°24.778'	69°13.002'	3470	N	ignimbrite	GX26814	13910	140	–23.8	16658	16663
39	511B	25°24.739'	69°12.742'	3450	N	ignimbrite	GX26841	14150	180	–24.2	16934	16940
40	510A	25°24.778'	69°13.002'	3450	N	ignimbrite	GX26825	16480	250	–23.5	19616	19621
42	499A	25°24.778'	69°13.002'	3470	N	ignimbrite	GX26823	40490	1630/1360	–23.5	—	—

^aIntercepts were obtained with Calib4.3 (Intcal98)—a 24-yr southern hemisphere deduction was applied.

^bMidpoints were obtained at 1σ.

2002). A comparative dietary study of two midden-forming rodents, *Lagidium viscacia* and *Abrocoma cinerea*, from the central Atacama (~23° 30' S; 3660 m) indicate that the former species has a poorly defined generalist diet whereas *Abrocoma* survives on very few species (Cortés *et al.*, 2002). Midden studies from the Monte Desert of northwestern Argentina indicate that midden-forming *Abrocoma* behaves as a dietary generalist.

In our study we lacked modern middens to compare with pollen rain soil samples, and therefore cannot directly estimate the relative under- or over-representation of each taxa within the midden matrix. Our most recent middens (<1000 yr BP) from the higher elevation site, however, match modern surface pollen assemblages at the same site (see Fig. 11). Given the very low plant productivity and pollen production in the area today, the midden pollen may be representative of a very local assemblage of plants around the sites. Some evidence does exist for extralocal, anemophilous species represented in these middens, as indicated by the very low presence of Podocarpaceae and *Alnus*. Today, these taxa occur 400 km to the east in cloud forests on the eastern flank of the subtropical Andes

(*Alnus*: middens 517, 528-B, 503-A, 499-B, 498-A and 510-A; Podocarpaceae: middens 526-B and 499-A; all percentages are <1%, data not shown).

Results

Radiocarbon ages of the middens

We obtained 37 radiocarbon dates on middens that span more than 50 000 years (Table 1). Nine middens dated between 0 and 2 k cal. yr BP, three between 2 and 10 k cal. yr BP, 18 between 10 and 24 k cal. yr BP, and seven middens were older than 33 k cal. yr BP. Of these oldest seven middens, only three returned finite dates. Given the excellent preservation and the relatively mesic pollen assemblages, we suspect that the 'infinite' age middens probably date to marine isotope stage (MIS) 4. We also note that our mid-elevation (3100–3200 m) series yielded no sample older than 8.4 k cal. yr BP, so the main

comparison in this paper is between our lower (Chaco I: 2670–2800 m) and upper elevation (Chaco III: 3450–3500 m) sites (Table 1).

Modern surface samples

Pollen percentages in soil surface samples from each site along our elevational transect is plotted in Fig. 5. Cluster analysis indicates three groups of samples designated as Modern Pollen Groups I, II and III.

Modern Pollen Group I

These assemblages include all the higher elevation samples dominated by High Andean steppe, including those collected along the Andes transect (Cerro Los Patitos) and along the western flank of the Cordillera de Domeyko. Within this group, three subgroups are identified.

Subgroup I-1 includes the four sites along the Andes transect that correspond to the upper Subnival belt, dominated by Poaceae (<40%), and Asteraceae *Chaetanthera*-type (~20–40%) as well as Apiaceae (to ~10%) and Verbenaceae (to ~50%). The latter two families most likely correspond to *Mulinum spinosum* and *Urbania pappigera*, respectively, which are important components of the modern vegetation. *Subgroup I-1* also includes pollen of extraregional taxa (i.e. *Alnus*), which blows in from Andean cloud forests several hundred kilometres to the east and northeast. *Subgroup I-2* includes sites from the higher elevations of the Cordillera de Domeyko, dominated by Poaceae (to 65%) and Fabaceae (~40%) pollen. Fabaceae pollen most likely comes from *Adesmia frigida* and *A. cf. hystrix*. The high grass pollen percentages in *Subgroups I-2 and I-3* probably denote the presence of more or less even cover of *Stipa frigida* across the extensive flatlands that border Quebrada del Chaco. *Subgroup I-3* includes sites in the Cordillera de Domeyko that are dominated by Poaceae with only low percentages of Asteraceae, Fabaceae and *Ephedra* sp.

Modern Pollen Group II

This cluster includes sites from the western flank of the Cordillera Domeyko and is characterised by predominantly lowered grass pollen (<5–70%), and an increase in importance of Verbenaceae (up to 70%) and Fabaceae (up to 56%). Two subgroups are evident. *Subgroup II-1* is characterised by high percentages of Poaceae (<70%) and Verbenaceae as well as Solanaceae and Brassicaceae at lower elevations; and *Subgroup II-2* is dominated by Fabaceae (~50%) and associated with Brassicaceae and Verbenaceae, such as *Acantholippia deserticola*, and low pollen percentages of *Ephedra*.

Modern Pollen Group III

These pollen samples were taken from soils surrounding springs. The samples display high percentages of Chenopodiaceae (>40%) with lesser amounts of Poaceae and Nollanaceae-*Lycium*. *Acaena magellanica* (40%; Rosaceae) and Cyperaceae (43%) are also dominant at Vega 2 in Quebrada del Chaco.

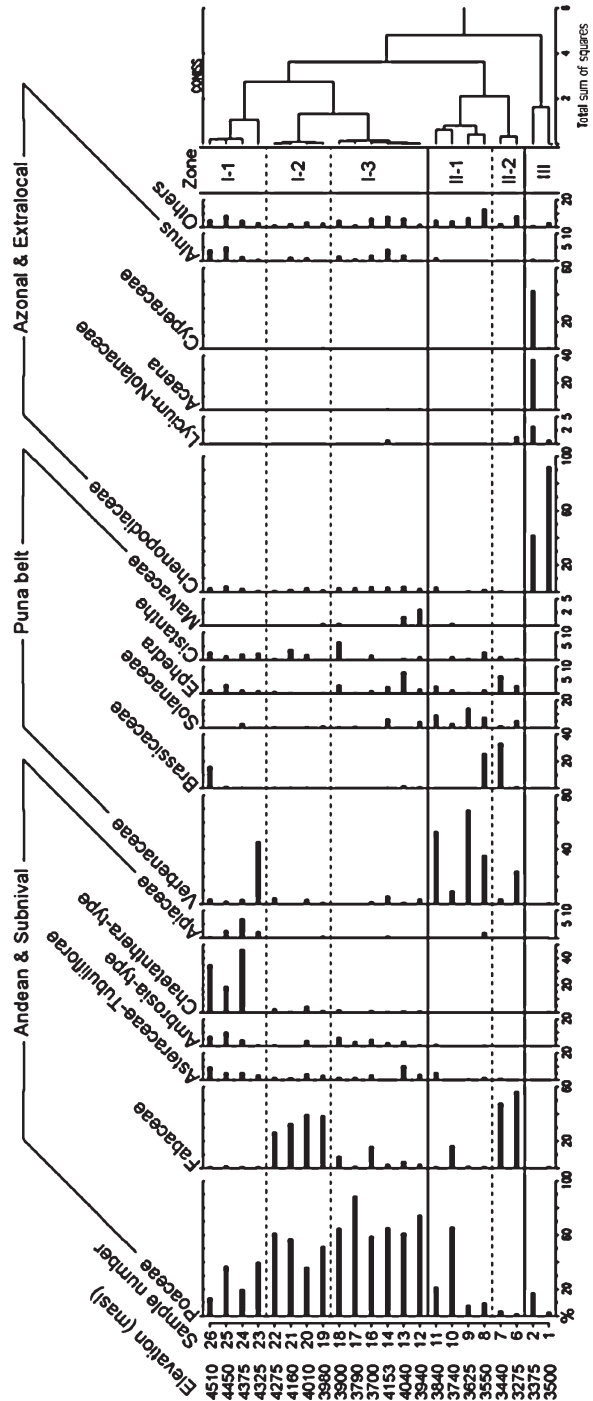


Figure 5 Frequency distribution of each taxon in modern surface pollen: 1–2; azonal wetlands; 6–14; Domeyko Cordillera; 16–26; High Andes, Cerro Los Patitos

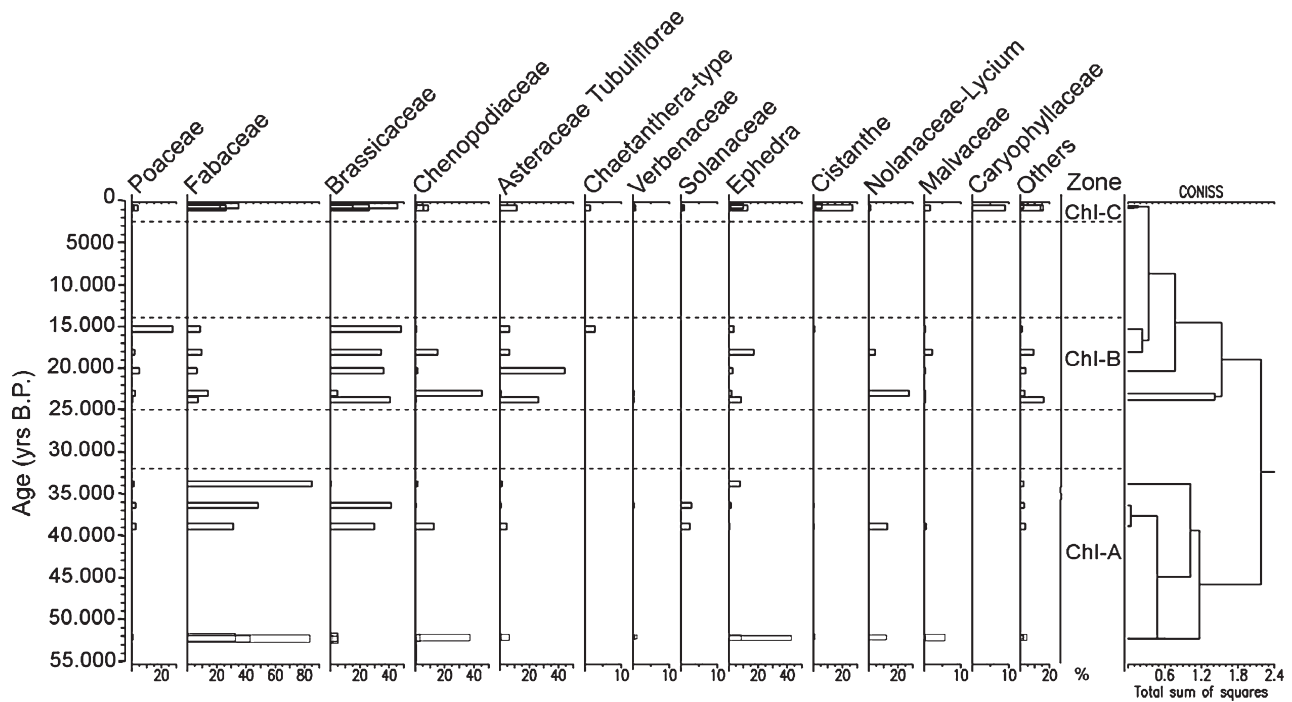


Figure 6 Fossil pollen diagram from the Chaco I middens at 2670–2800 m a.s.l.

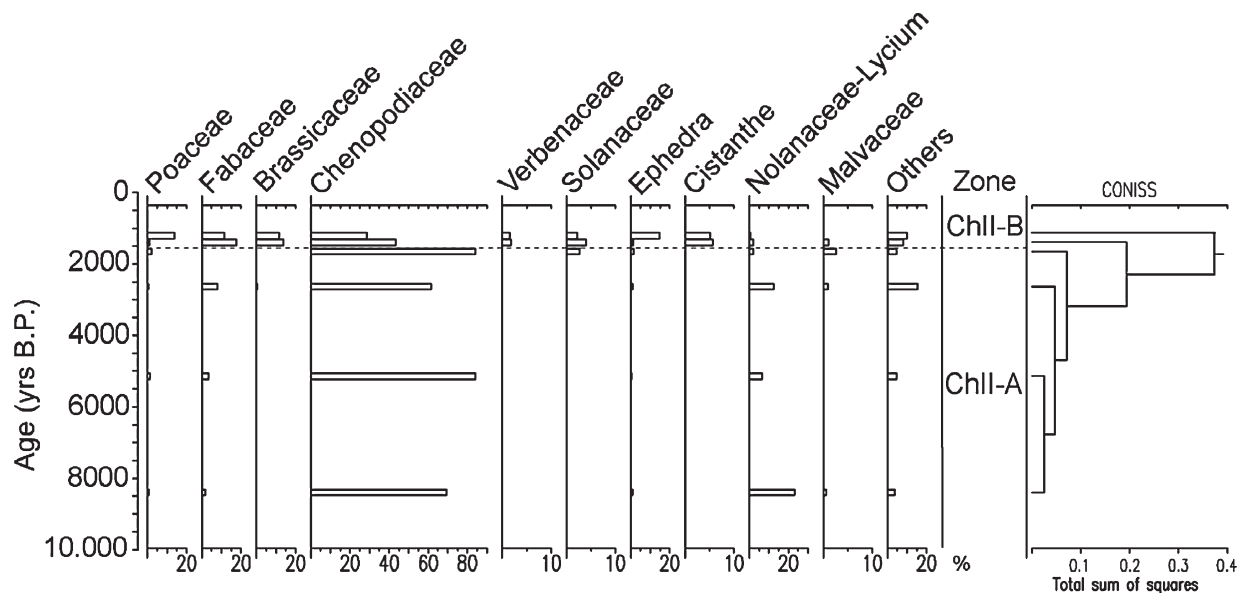


Figure 7 Fossil pollen diagram from the Chaco II middens at 3100–3200 m a.s.l.

Fossil midden pollen records

Chaco I (2670–28 000 m) (Fig. 6)

Sixteen middens were analysed from a local travertine outcrop and a Miocene fanglomerate near the mouth of Quebrada del Chaco. The travertine outcrop incorporated the oldest middens in the record, dating back to the previous interstadial (>50 to 33 k cal. yr BP) and to the full glacial period (24–15 k cal. yr BP). Three different zones were recognised in the CONISS analysis (Fig. 6). *Zone Ch I-A* spans middens that date between >50 to 33 kyr BP, and is characterised by high percentages of Fabaceae pollen (30–85%). Other taxa include Brassicaceae (to ~42%), Chenopodiaceae (to ~37%) and *Ephedra* (to ~43%). No middens were recovered from the period 33–25 k cal. yr BP.

Zone Ch I-B includes middens from the full glacial period (24–15 k cal. yr BP). All middens display a reduction in

Fabaceae pollen (7–14%) and a concomitant increase in Brassicaceae (to ~50%). Chenopodiaceae are frequent although variable in amount (max. 46%) as well as Asteraceae-Tubuliflorae (max. 26%), Nolanaceae-Lycium (max. 28%) and *Ephedra* (between 2% and 17%). The youngest middens have high percentages of Poaceae (~25%). There is large hiatus in this midden series between 15 and 1.0 k cal. yr BP.

Zone Ch I-C includes middens dated to the last 1500 cal. yr BP. Midden pollen is dominated by Fabaceae (between 22% and 35%) and Brassicaceae (between 15% and 46%). Other associated taxa are Asteraceae-Tubuliflorae (max. 12%), Chenopodiaceae (max. 9%), *Ephedra* (max. 13%) and *Cistanthe* (max. 27%).

Chaco II (3100–3200 m) (Fig. 7)

Six middens were collected from crevices in either Miocene fanglomerate or a second isolated outcrop of travertine. *Zone*

Ch II-A includes four middens dating to between 9 and 1.5 k cal. yr BP, and are dominated by Chenopodiaceae (60–85%) with the presence of Nolanaceae-*Lycium* (max. 23%). *Zone Ch II-B* includes two late Holocene middens (<1500 cal. yr BP) dominated by Chenopodiaceae (29–43%). Fabaceae (11–18%) and Brassicaceae (12–14%) appear in somewhat lesser amounts, but are clearly more important than in *Zone II-A*.

Chaco III (3450–3500 m) (Fig. 8)

Seventeen middens were collected in ignimbrite outcrops near the head of Quebrada del Chaco, and include those dated 20–11 k cal. yr BP and 40.5 k cal. yr BP. Our cluster analysis distinguishes two pollen zones consisting of (a) the full glacial middens and (b) the Late Glacial and Holocene middens. *Zone Ch III-A* consists of one midden dated to 40.5 k cal. yr BP, and dominated by Asteraceae-Tubuliflorae (>65%) and low amounts of Poaceae (15%). *Zone Ch III-B* middens had elevated though variable amounts of Poaceae (max. 77%) and Asteraceae-Tubuliflorae (max. 54%). Also present are Chenopodiaceae (max. 44%), and Asteraceae *Chaetanthera*-type (max. 35%). *Zone Ch III-C* middens are dominated by Asteraceae-Tubuliflorae (14–51%) associated with Poaceae (7–25%) and Brassicaceae (max. 26%). *Zone Ch III-D* includes two early and mid-Holocene middens. Both samples are dominated by azonal (riparian) elements, as represented by Chenopodiaceae (28–56%) and Nolanaceae-*Lycium* (max. 40%). *Zone Ch III-E* has three late Holocene middens dating to the last 1000 cal. yr BP and having elevated percentages of Fabaceae (~30%) and Brassicaceae (max. 53%). Several other taxa are present but in low percentages.

The relationship between modern surface and fossil midden pollen

In order to express the degree of relatedness between pollen assemblages in modern soil samples and fossil middens, we constructed dendrograms of the combined data for any taxon with pollen percentages that equal or exceed 5%. This yielded 15 taxa for comparisons among modern soil samples, 17 (Chaco I), 18 (Chaco II) and 20 (Chaco III) taxa for comparisons between modern soil samples and fossil middens, and 10 (Chaco I), 8 (Chaco II) and 13 (Chaco III) taxa for comparisons among fossil middens.

Chaco I (2670–2800 m)

The Chaco I data group into three clusters (Fig. 9). The first and most isolated cluster includes the two pollen samples from localised wetlands. The second cluster includes all of the modern pollen samples collected along the vegetation transect, excluding the samples at the lower vegetation limit (3275 and 3440 m). These latter pollen samples are integrated in a third cluster that includes all of the fossil pollen spectra from the Chaco I record. The dendrograms suggest that Pleistocene pollen assemblages are representative of vegetation now found ~700 m above the midden sites. We note that middens dated to less than 1000 cal. yr BP are also included in this category.

Chaco II (3100–3200 m)

Two main clusters are readily seen in Fig. 10. The first cluster incorporates all the pollen rain samples analysed along our

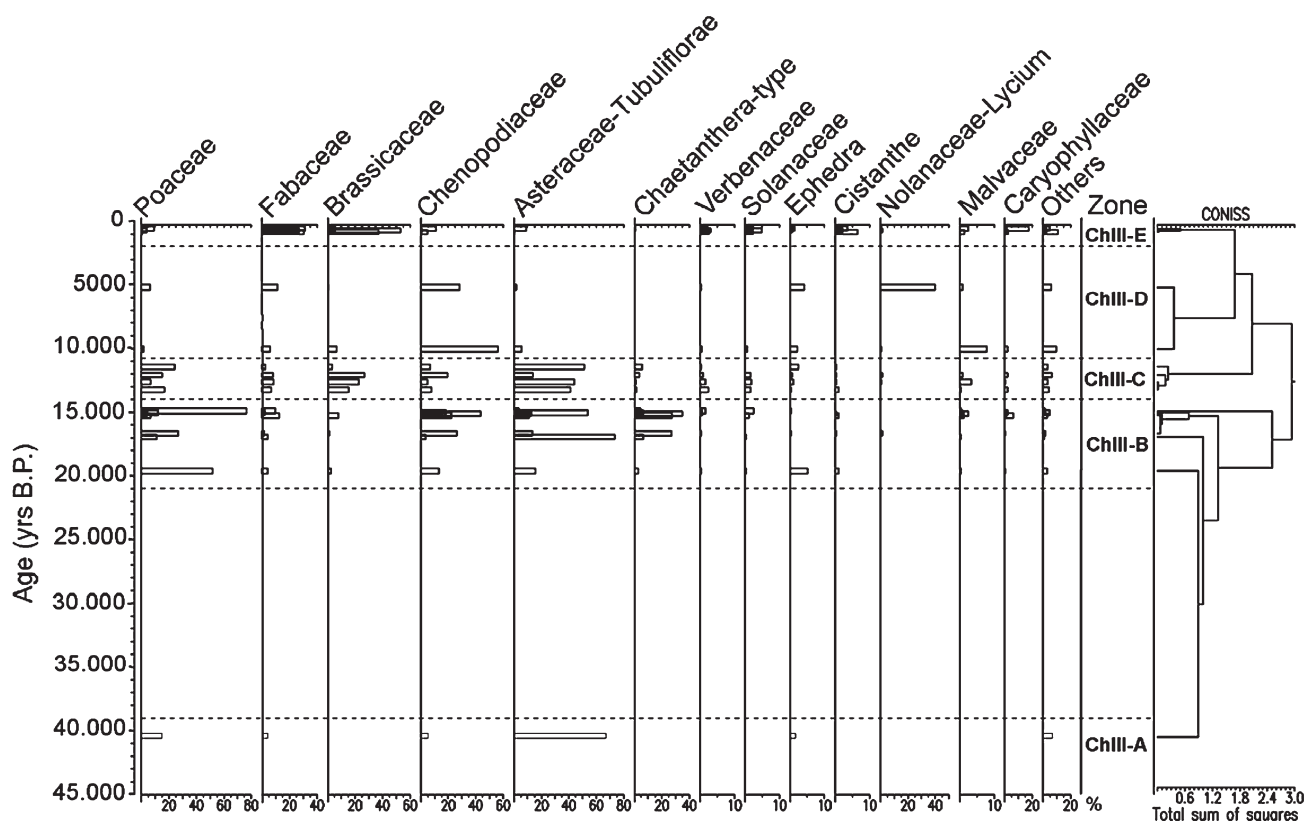


Figure 8 Fossil pollen diagram from the Chaco III middens at 3450–3500 m a.s.l.

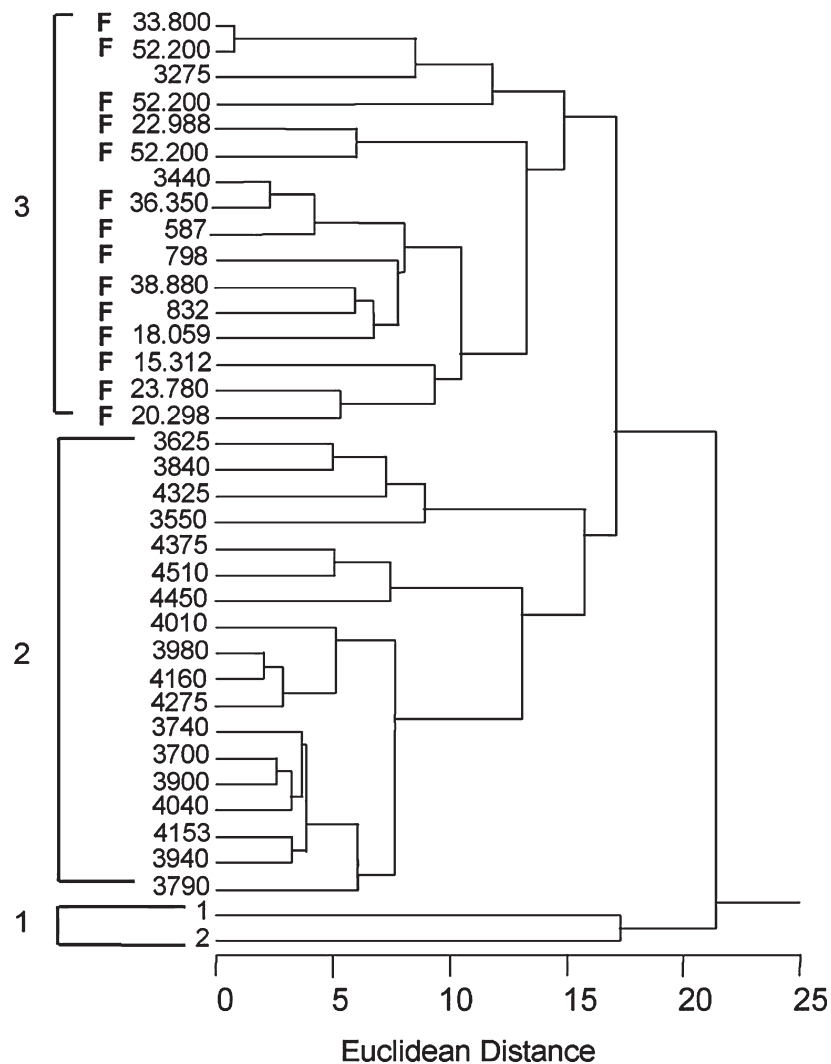


Figure 9 Dendrogram expressing relatedness among modern surface pollen samples along transect and Chaco I (2670–2800 m) midden pollen assemblages. Groups are highlighted with numbers. Midden pollen spectra with their corresponding age are named with the letter 'F'. Elevation is indicated for modern surface pollen assemblages for zonal vegetation. Numbers 1 and 2 represent the two spectra for azonal pollen rain

main zonal vegetation transect. The second cluster groups all the mid- and late Holocene fossil middens with the azonal (wetland) pollen rain samples, especially with those from Vega 1, taken from one of the many small springs along the western margin of Salar de la Azufrera. This indicates that for most of the Holocene, the vegetation near these middens was not analogous to that of the surrounding zonal (hillslope or 'pampa') vegetation but rather, was closer to the azonal (riparian) vegetation found today along modern springs and seeps. This can be explained by a hyperarid climate that would have limited plant growth to point sources of permanent water, such as those found at Vegas del Chaco and Salar de la Azufrera.

Chaco III (3450–3500 m)

Seven clusters are clearly distinguishable in Fig. 11. The first two clusters show no relationship between fossil and modern pollen. The first cluster includes modern samples whereas the second cluster includes middens dated between 17 and 11 k cal. yr BP, as well as a sample dated at 40.5 kyr BP. The second cluster may indicate a lack of modern analogue, at least locally. The third cluster groups middens dated between 17 and 15 kyr BP with modern pollen rain samples from the

highest elevations of our vegetation transect, more than 1000 m above the midden sites. The fourth cluster includes Late Glacial and late Holocene middens with pollen rain samples collected at similar to slightly lower altitudes than the midden sites. The fifth cluster includes only modern pollen rain samples. The sixth group clusters two late glacial samples with pollen rain samples collected at least 200 m above the midden sites. The seventh cluster includes a Holocene midden with the pollen rain samples collected at the localised wetlands. Only one midden sample from the mid-Holocene did not cluster with any of the modern pollen rain samples.

Discussion

By way of summary, pollen percentages from the different taxa identified in the three fossil midden series were aggregated and plotted by their actual occurrence in each of the modern vegetation belts (Fig. 12). For each of the pollen zones across all three elevations, we inferred more humid conditions (H) or equally arid (A) as today. We inferred wetter winters or summers due to either increased westerlies (W) or easterlies (E), respectively, and based on (a) the nature of in the pollen

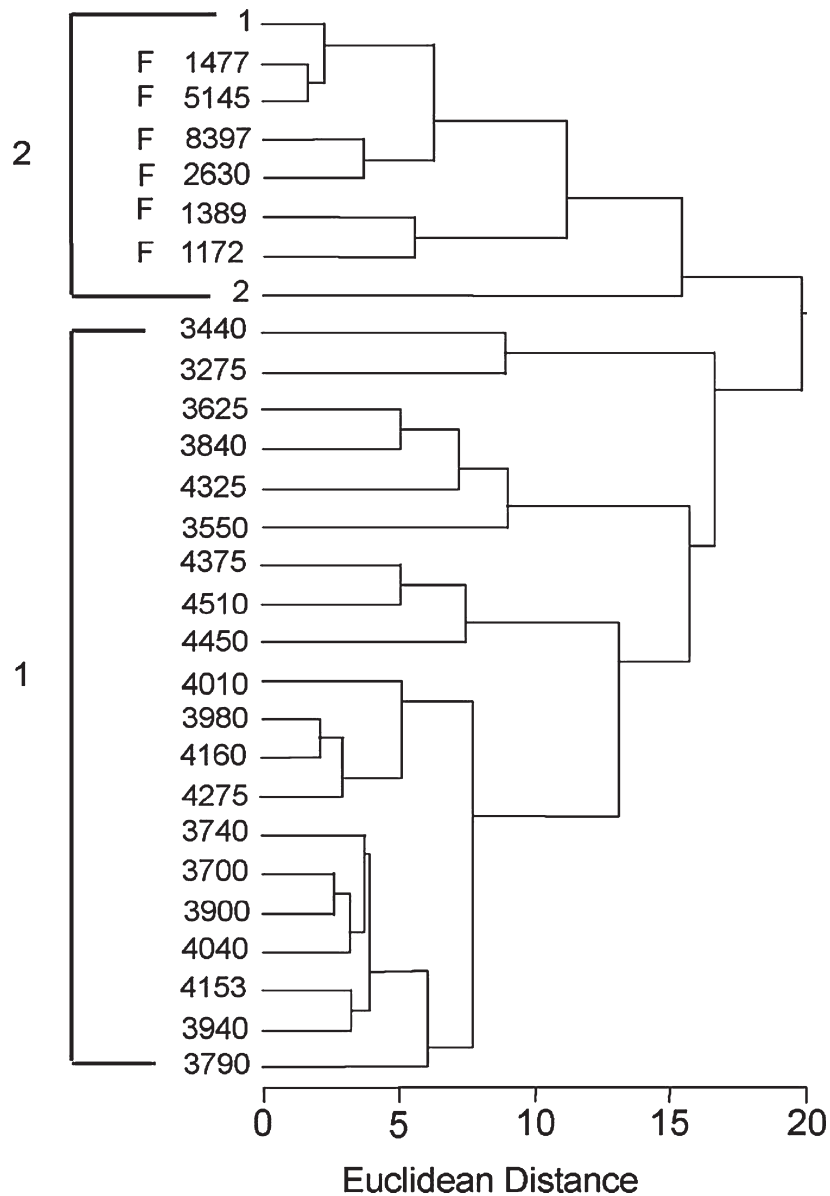


Figure 10 Dendrogram expressing relatedness among modern surface pollen samples along transect and Chaco II (3100–3200 m) midden pollen assemblages. Groups are highlighted with numbers. Midden pollen spectra with their corresponding age are named with the letter ‘F’. Elevation is indicated for modern surface pollen assemblages for zonal vegetation. Numbers 1 and 2 represent the two spectra for azonal pollen rain

assemblages, (b) whether the changes happened only at high (summer), or at low or all elevations (winter), and (c) the timing of wet and dry phases in other records to the north and south of Quebrada del Chaco. There is at least one period (33–25 k cal. yr BP) with a prolonged gap in midden deposition and possibly a drop in plant productivity. In Fig. 12, we label it as potentially dry (D?) but we caution that these gaps may or may not imply reduced plant productivity and rodent activity. The Quebrada del Chaco record is very fragmentary owing to the discontinuous and sporadic nature of the midden record, and should be taken only as a first approximation pending replication and better temporal coverage.

Assuming that all of our ‘infinite’ age middens (>52, >38.8, >36.4, and >33.8 k ¹⁴C yr BP) actually date between 75 and 33 kyr BP, and that the three finite dates (37.3, 40.5 and 45.8 kcal. yr BP) are accurate, winter precipitation was much higher than today during the early glacial period at least during the times of documented midden deposition. Contamination from younger carbon is a problem with samples near the limits of the radiocarbon method, and would not have been resolved by our routine pretreatment of the Quebrada del Chaco

samples. The contamination problem can now be avoided, however, through (a) an invasive chemical pretreatment and stepped-combustion techniques to remove contaminants; (b) a modified extraction system that reduces the amount of atmospheric CO₂ introduced into the sample during processing (Bird *et al.*, 1999). We hope eventually to resolve whether or not all of the early glacial dates could be finite up to ~55 kyr BP, allowing correlations with other pluvial evidence available for MIS 3 (i.e. Lamy *et al.*, 1998).

The wettest period in the midden series at all three elevations, and presumably the greatest extension of the southern westerlies, was 24–15 k cal. yr BP. During this time the Subnival taxon *Chaethantera*, which today is not registered in pollen assemblages below 3700 m and is well represented only above 4350 m, shows up in fossil middens as traces at 2670–2800 m (Chaco I) and as high percentages between 3450–3500 m (Chaco III). Both midden series imply a 1000 m lowering of species distributions. The high percentages of grass pollen in Chaco III suggest that a diffuse cover of *Stipa frigida* blanketed the now-plantless ‘pampas’ at 3500 m; the lower grass percentages in Chaco I (except in one sample at 15 k cal. yr BP)

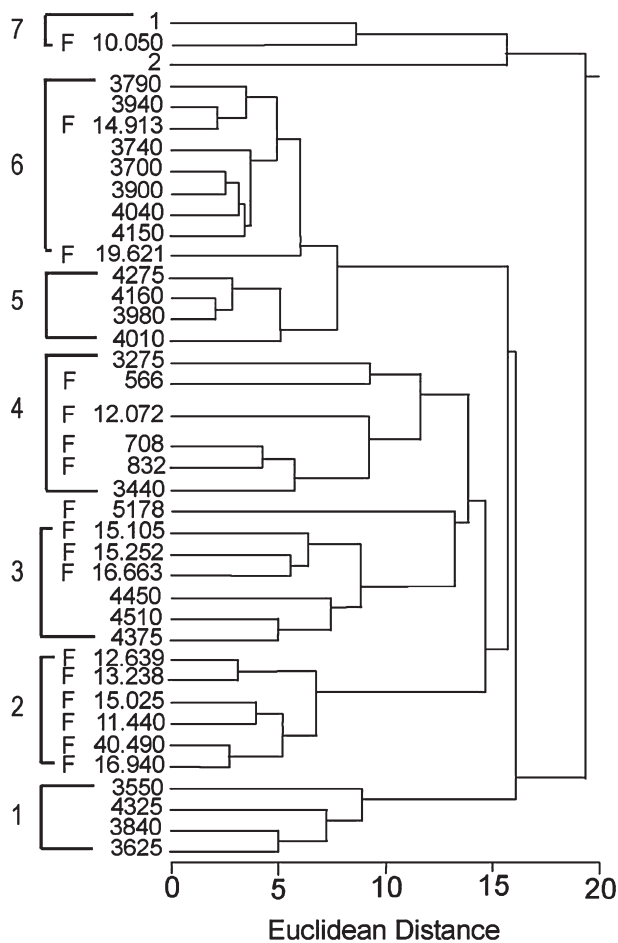


Figure 11 Dendrogram expressing relatedness among modern surface pollen samples along transect and Chaco III (3450–3500 m) midden pollen assemblages. Groups are highlighted with numbers. Midden pollen spectra with their corresponding age are named with the letter 'F'. Elevation is indicated for modern surface pollen assemblages for zonal vegetation. Numbers 1 and 2 represent the two spectra for azonal pollen rain

indicate that this diffuse grassland gave way to absolute desert somewhere between 3500 and 2670 m, again a displacement of the modern limits of continuous vegetation of at least 1000 m. Cluster analysis grouped midden assemblages dated between 17 and 15 kyr BP from Chaco III with modern pollen rain samples from the highest elevations (4375–4450 m) in our vegetation transect, more than 1000 m above the midden sites. Accordingly, this was probably the wettest interval in the full glacial period for which we have documented midden deposition.

Between 15 and 11 k cal. yr, the midden series at the highest elevation (Chaco III) suggests regional drying and as much as 500–700 m upward retreat of vegetation. It is likely that the diffuse plant cover that occupied the 'pampas' for a few hundred metres below the Chaco III midden sites 'contracted' to Quebrada del Chaco during the Late Glacial. This Late Glacial period, nevertheless, remained wetter than today with assemblages indicative of modern vegetation 200 m above the midden sites. We suspect that this slight lowering of vegetation relative to modern may have been supported by southwestward extension of well-documented summer pluvial conditions that existed only 200–250 km to the north in the central Atacama (Betancourt *et al.* 2000; Latorre *et al.* 2002, 2003).

The pollen record from 11 to 1.0 k cal. yr BP is essentially modern, though the temporal coverage of the middens was

poor at all three elevations in Quebrada del Chaco. The most interesting Holocene pollen record is from three middens dated at 0.6–0.8 k cal. yr BP, which suggests an unusual wet interval at our lowest site (Chaco I). Because it was registered at our lowest elevation, we suspect that this was due to a period of unusually wet winters that were sufficiently long to allow for dispersal and recruitment of perennial shrubs and *Stipa frigida* at this hyperarid site.

Comparison with other records in the region

The nearest palaeohydrological record to Quebrada del Chaco is from a 40 m long sediment core, dated using the U-series isochron method, at Salar del Hombre Muerto (25° 20' S, 67° W) in the Argentinean Andes 150 km east of Quebrada del Chaco. Saline lake (82–75, 64, 57–55 and 45 k cal. yr BP) and saline pan (49, 44–38 and 24–20 k cal. yr BP) halites record very wet and moderately wet phases, respectively (Godfrey *et al.*, 2003). Two hundred kilometres north of Quebrada del Chaco a 100-m and 100-kyr long salt core from Salar de Atacama (23° S, 68° W), records the prevalence of wet conditions, in the form of saline lakes and expanded mudflats, at 75.8–60.7 k cal. yr BP and from 54.0 to 15.2 k cal. yr BP (Bobst *et al.*, 2001). A marine sedimentary record from the Pacific Coast (27.5° S), which uses mineralogical and grain size data to infer sediment contributions from the Andes proper, indicates two prolonged wet phases centred on 50 and 22 k cal. yr (Lamy *et al.*, 1998). This also matches pollen records from Laguna Tagua-Tagua (34° 30' S) (Heusser, 1983, 1990), the Chilean Lake District and Chiloé Island (39°–43° S) (Heusser *et al.*, 1999; Villagrán *et al.*, 2004), and makes a case for northward expansion of the southern westerlies ~57–40 k cal. yr BP, and again between 24 and 15 k cal. yr BP.

Given a 1000-m lowering of plant distributions at Quebrada del Chaco, however, we would expect that wetter winters during early (>24 k cal. yr BP) to full glacial (24–15 k cal. yr BP) times might have extended as far north as the Calama Basin and Salar de Atacama (22–24° S). If they were confined to the lower elevations, such increases in winter precipitation are probably not enough to explain the early to full glacial saline lake phases at Salar de Atacama. Few other records actually span the early to full glacial in this region. With the exception of fossil middens, most of the regional palaeohydrological records are from the highest elevations, where regional increases in winter precipitation may or may not register at more northerly latitudes. Except for the large saline lake phases at Salar de Atacama (Bobst *et al.*, 2001), the general consensus from multiple lines of evidence is for maximum pluvial conditions to have occurred in the central Atacama with strengthening of the tropical easterlies in the late glacial (15–10 kyr BP) period (Geyh *et al.*, 1999; Grosjean *et al.*, 2001; Betancourt *et al.*, 2000; Latorre *et al.*, 2002, 2003; Rech *et al.*, 2002).

The Late Glacial to early Holocene is marked by rapid deglaciation in southern Chile and increasing aridity and temperature in central Chile (Denton *et al.*, 1999; Heusser *et al.*, 1999; Moreno, 1997; Moreno *et al.*, 1999; Villagrán, 1988a, 1988b; Lamy *et al.*, 1999; Jenny *et al.*, 2003). This suggests contraction of the southern westerlies and winter storm tracks to the south. Conversely, the period 13.5–9.6 k cal. yr BP was characterised by higher lake (Grosjean 1994; Geyh *et al.* 1999) and ground water levels (Rech *et al.* 2002) in the central Atacama (22–24° S). The rodent midden record from this area indicates lowering of some plant distributions by up to 900 m, while the presence of summer annuals in the midden assemblages indicate that the wetting occurred primarily in summer

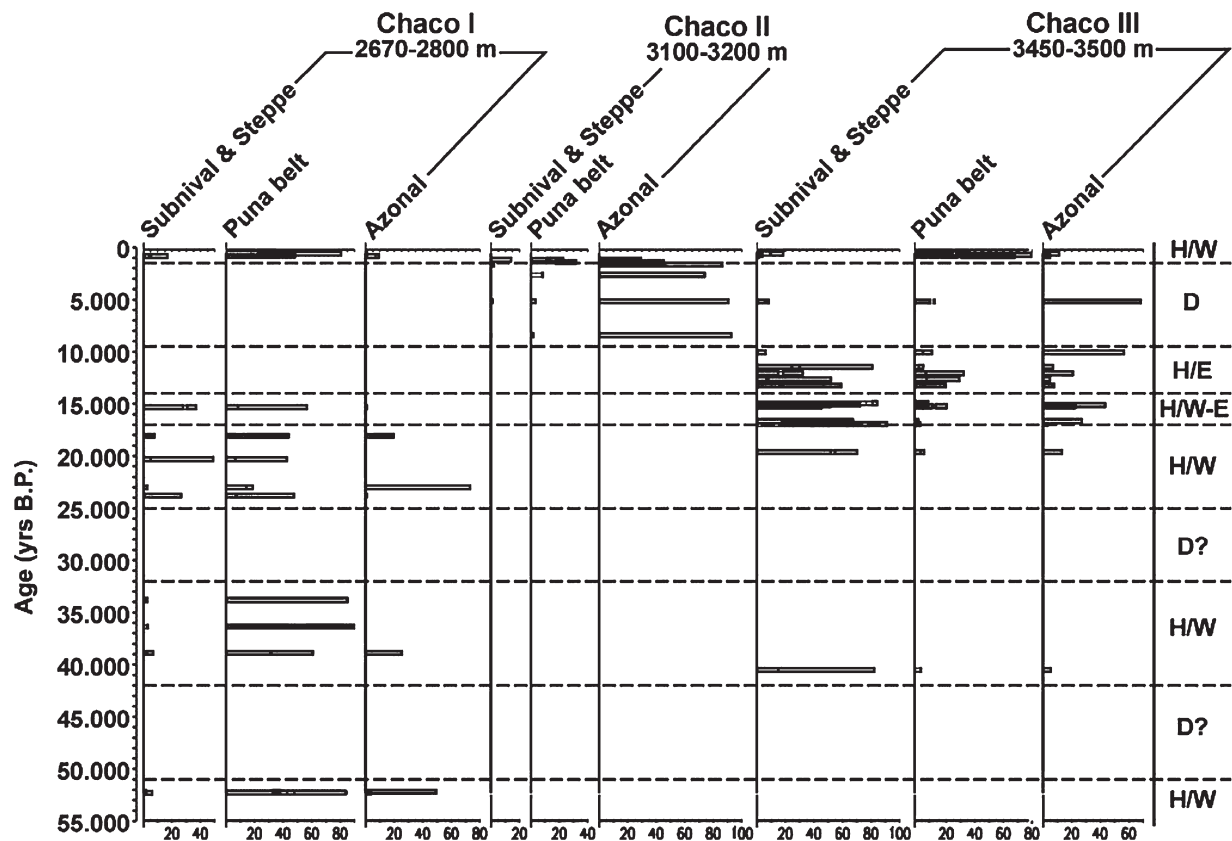


Figure 12 Diagram showing the pollen percentages for each taxon in the three fossil records. They are aggregated as subnival–steppe, puna and azonal. On the right-hand side, we provide the climatic interpretation: W: wetter winters due to expanded southern westerlies; E: wetter summers due to stronger easterlies; A: arid; H: humid

(Betancourt *et al.*, 2000; Latorre *et al.*, 2002). The implication is that the increases in convective, summer rains were not confined to the highest elevations and extended at least as far down as 2400 m at the southeastern end of Salar de Atacama. We note that these sites are much closer in horizontal distance to the crest of the Andes than Quebrada del Chaco.

Given the incompleteness of the Holocene fossil record at Quebrada del Chaco, this leaves for final discussion our evidence at Chaco I (our lowest site) for a mini-pluvial event in the last millennium. The only corroborating evidence thus far is from a pollen record indicating increasingly wetter conditions along the Chilean coast at 32° S (Maldonado and Villagran, 2002). Given the apparent magnitude of this event at Quebrada del Chaco, which lies near the maximum extent of the southern westerlies, we anticipate that this mini-pluvial will eventually show up in myriad records in the southern Atacama and points south.

Conclusions

Fossil rodent middens have quickly become the primary source of information about late Quaternary vegetation in the Atacama Desert but until now have involved just plant macrofossil analyses (Betancourt *et al.*, 2000; Holmgren *et al.*, 2001; Latorre *et al.*, 2002, 2003). Quebrada del Chaco is the first midden study to involve pollen analysis, and it has proven to be a stand-alone record that can be interpreted independently of the plant macrofossil assemblages. This has not always been the case with fossil rodent middens studies in North America and elsewhere (Pearson and Betancourt, 2002). In the Atacama, the

usefulness of the pollen record is enhanced by a relatively simple flora; a scarcity of wind-pollinated taxa; the ability for the pollen to resolve a sharp ecotone between diffuse (zonal) and ‘contracted’ vegetation (azonal) at ~3900–4000 m; and an overall steep gradient of well-defined pollen assemblages with elevation. These circumstances allowed us to pinpoint the displacement of indicator species and the elevation at which diffuse vegetation formerly covered the expansive and now plantless ‘pampas’ bordering Quebrada del Chaco.

During several intervals in the early and full glacial periods, northern constraints on the southern westerlies and winter storm tracks must have relaxed enough to produce wetter conditions and lowering of plant distributions. Without an adequate array of weather stations and long-term precipitation records with elevation in the southern Atacama, it is difficult to quantify precipitation changes associated with a 1000 m lowering of plant distributions and vegetation patterns. Unlike plant zonation elsewhere in the Americas, growing season temperatures have little effect on effective moisture and lower plant limits in the Atacama Desert. The displacement of lower limits at Quebrada del Chaco then is a function of changes in the abundance of seasonal precipitation. When compared to other records south (winter) and north (summer), the most parsimonious explanation is that increasing winter precipitation produced the early and full glacial wet events at Quebrada del Chaco, while increasing summer precipitation may explain the slight lowering of vegetation in the Late Glacial period. Winter and summer wet events, and by extension changes in the strengths of the westerlies and easterlies, were apparently antiphased. An exception may have been the transition from full to Late Glacial conditions. The paucity of Holocene middens at all three elevations in Quebrada del Chaco suggest that there must have been few periods sufficiently wetter than today

for long enough to have caused even minor displacements of vegetation in the last 10 000 years. The one exception is a wet event in the last millennium, which we expect to be replicated by ongoing and future palaeoclimatic studies in the southern Atacama.

Acknowledgements The authors wish to thank Carolina Soto for assistance in the field, Kate Aasen Rylander for assistance in the laboratory, and Martin Grosjean, Scott Anderson and Associate Editor Don Rodbell for thoughtful reviews. Funding for this study was provided by Doctoral Scholarship Grant CONICYT-FONDECYT-2000026 and FONDECYT Grant- 3030026 to C.L. and NSF-ESH EAR-9904838. We also thank the Millennium Center for Advanced Studies in Ecology and Research on Biodiversity (P02-051-F ICM) for ongoing support.

References

- Anderson RS, Van Devender TR. 1991. Comparison of pollen and macrofossils in packrat (*Neotoma*) middens: a chronological sequence from the Waterman Mountains of southern Arizona, U.S.A. *Review of Palaeobotany and Palynology* **68**: 1–28.
- Argollo J, Mourguiart P. 2000. Late Quaternary climate history of the Bolivian Altiplano. *Quaternary International* **72**: 37–51.
- Arroyo MTK, Squeo FA, Armesto JJ, Villagrán C. 1988. Effects of aridity on plant diversity in the northern Chilean Andes: results of a natural experiment. *Annals of the Missouri Botanical Garden* **75**: 55–78.
- Arroyo MTK, Castor C, Marticorena C, Muñoz M, Cavieles L, Mathei O, Squeo F, Grosjean M, Rodríguez R. 1998. The flora of Lullailaco National Park located in the transitional winter–summer rainfall area of the northern Chilean Andes. *Gayana Botánica* **55**: 93–110.
- Baker PA, Grove M, Cross S, Seltzer G, Fritz S, Dunbar R. 2001. The history of South American tropical precipitation for the past 25,000 years. *Science* **291**: 640–643.
- Betancourt JL, Saavedra B. 2002. Paleomadrigueras de roedores, un nuevo método paleoecológico para el estudio del Cuaternario en zonas áridas en Sudamérica. *Revista Chilena de Historia Natural* **75**: 527–546.
- Betancourt JL, Latorre C, Rech JA, Quade J, Rylander KA. 2000. A 22,000-year record of monsoonal precipitation from northern Chile's Atacama Desert. *Science* **289**: 1542–1546.
- Betancourt JL, Rylander KA, Peñalba C, McVicker JL. 2001. Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **165**: 71–95.
- Bird MI, Ayliffe LK, Fifield LK, Turney CSM, Cresswell RG, Barrowys TT, David BB. 1999. Radiocarbon dating of 'old' charcoal using a wet oxidation-stepped combustion procedure. *Radiocarbon* **41**: 127–140.
- Bobst AL, Lowenstein TK, Jordan TE, Godfrey LV, Hein MC, Ku TL, Luo S. 2001. A 106 ka paleoclimate record from drill core of the Salar de Atacama, northern Chile. *Palaeogeography, Palaeoclimatology, Palaeoecology* **173**: 21–42.
- Clapperton CM, Clayton JD, Benn DI, Marden CJ, Argollo J. 1997. Late Quaternary glacier advances and palaeolake highstands in the Bolivian Altiplano. *Quaternary International* **38/39**: 49–59.
- Cortés A, Rau JR, Miranda E, Jiménez JE. 2002. Hábitos alimenticios de *Lagidium viascacia* y *Abrocoma cinerea*: roedores sintópicos en ambientes altoandinos del norte de Chile. *Revista Chilena de Historia Natural* **75**: 583–593.
- Davis OK, Anderson RS. 1987. Pollen in packrat (*Neotoma*) middens: pollen transport and the relationship of pollen to vegetation. *Palynology* **11**: 185–198.
- Davis OK, Anderson RS. 1988. Reply to Discussion, T.R. Van Devender. *Palynology* **12**: 226–229.
- Denton GH, Lowell TV, Heusser CJ, Schlüchter C, Anderson BG, Heusser LE, Moreno PI, Marchant DR. 1999. Geomorphology, stratigraphy, and radiocarbon chronology of Llanquihue drift in the area of the southern Lake District, Seno Reloncaví, and Isla Grande de Chiloé, Chile. *Geografiska Annaler* **81**: 167–229.
- Faegri K, Iversen J. 1989. *Textbook of Pollen Analysis*. Blackwell: Oxford.
- Fornari M, Risacher F, Féraud G. 2001. Dating of paleolakes in the central Altiplano of Bolivia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **172**: 269–282.
- Fritz SC, Baker PA, Lowenstein TK, Seltzer GO, Rigsby CA, Dwyer GS, Tapia PA, Arnold KK, Ku T-L, Luo S. 2004. Hydrologic variation during the last 170,000 years in the southern hemisphere tropics of South America. *Quaternary Research* **61**: 95–104.
- Garleff K, Shäbitz H, Stingl H, Veit H. 1991. Jungquartäre Landschaftsentwicklung und Klimageschichte beiderseits der Ariden Diagonale Südamerikas. *Bamberger Geografisches Schriften* **11**: 367–369.
- Garreaud R, Aceituno P. 2002. Atmospheric circulation over South America: mean features and variability. In *The Physical Geography of South America*, Veblen T, Orme A, Young K (eds). Oxford University Press: Oxford.
- Garreaud R, Vuille M, Clement A. 2003. The climate of the Altiplano: observed current conditions and mechanisms of past changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**: 5–22.
- Geyh MA, 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). *Quaternary Research* **52**: 143–153.
- Godfrey LV, Jordan TE, Lowenstein TK, Alonso RL. 2003. Stable isotope constrains on the transport of water to the Andes between 22° and 26°S during the last glacial cycle. *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**: 299–317.
- Grimm E. 1987. CONISS: a fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* **5**: 13–35.
- Grosjean M. 1994. Paleohydrology of the Laguna Lejía (north Chilean Altiplano) and climatic implications for late-glacial times. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**: 89–100.
- Grosjean M, van Leeuwen JFN, van der Knaap WO, Geyh MA, Ammann B, Tanner W, Messerli B, Veit H. 2001. A 22,000 ¹⁴C year BP sediment and pollen record of climate change from Laguna Miscanti (23° S), northern Chile. *Global and Planetary Change* **28**: 35–51.
- Hajek ER, di Castri F. 1975. *Bioclimatografía de Chile*. Dirección de Investigación Universidad Católica de Chile: Santiago.
- Heusser CJ. 1983. Quaternary pollen record from Laguna de Tagua Tagua, Chile. *Science* **219**: 1429–1431.
- Heusser CJ. 1989. Southern westerlies during the last glacial maximum. *Quaternary Research* **31**: 423–425.
- Heusser CJ. 1990. Ice age vegetation and climate of subtropical Chile. *Palaeogeography, Palaeoclimatology, Palaeoecology* **80**: 107–127.
- Heusser CJ, Lowell TV, Heusser LE, Hauser A, Björn G. 1996. Full-glacial–late-glacial palaeoclimate of the Southern Andes: evidence from pollen, beetle, and glacial records. *Journal of Quaternary Science* **11**: 173–184.
- Heusser CJ, Heusser LE, Lowell TV. 1999. Paleocology of the southern Chilean Lake District-Isla Grande de Chiloé during middle-late Llanquihue glaciation and deglaciation. *Geografiska Annaler* **81**: 231–284.
- Holmgren C, Betancourt JL, Rylander KA, Roque J, Tovar O, Zeballos H, Linares E, Quade J. 2001. Holocene vegetation history from fossil rodent middens near Arequipa, Peru. *Quaternary Research* **56**: 242–251.
- Houston J, Hartley AJ. 2003. The Central Andean west-slope rainshadow and its potential contribution to the origin of hyper-aridity in the Atacama Desert. *International Journal of Climatology* **23**: 1453–1464.
- Jenny B, Wilhelm D, Valero-Garcés BL. 2003. The Southern Westerlies in Central Chile: Holocene precipitation estimates based on a water balance model for Laguna Aculeo (33° 50' S). *Climatic Dynamics* **20**(2/3): 269–280.
- King JE, Van Devender TR. 1977. Pollen analysis of fossil packrat middens from the Sonoran Desert. *Quaternary Research* **8**: 191–204.

- Lamy F, Hebbeln D, Wefer G. 1998. Late Quaternary precessional cycles of terrigenous sediment input off the Norte Chico, Chile (27.5° S) and paleoclimatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**: 233–251.
- Lamy F, Hebbeln D, Wefer G. 1999. High-resolution marine record of climatic change in mid-latitude Chile during the last 28,000 years based on terrigenous sediment parameters. *Quaternary Research* **51**: 83–93.
- Latorre C. 2002. Clima y vegetación del Desierto de Atacama durante el Cuaternario tardeó, II Región, Chile. Unpublished Ph.D. thesis, Universidad de Chile.
- Latorre C, Betancourt JL, Rylander KA, Quade J. 2002. Vegetation invasions into absolute desert: a 45 000 yr rodent midden record from the Calama–Salar de Atacama basins, northern Chile (lat 22°–24° S). *Geological Society of America Bulletin* **114**: 349–366.
- Latorre C, Betancourt JL, Rylander KA, Quade J, Matthei O. 2003. A 13.5-kyr vegetation history from the arid prepuna of northern Chile (22–23° S). *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**: 223–246.
- Maldonado A, Villagrán C. 2002. Paleoenvironmental changes in the semiarid coast of Chile (~32° S) during the last 6200 cal years inferred from a swamp-forest pollen record. *Quaternary Research* **58**: 130–138.
- Markgraf V, Dodson JR, Kershaw AP, McGlone MS, Nicholls N. 1992. Evolution of late Pleistocene and Holocene climates in the circum-South Pacific land areas. *Climate Dynamics* **6**: 193–211.
- Marticorena C, Matthei O, Rodríguez R, Kalin Arroyo MT, Muñoz M, Squeo F, Arancio G. 1998. Catalogo de la flora vascular de la Segunda Región (Región de Antofagasta), Chile. *Gayana Botánica* **55**: 23–83.
- Monod T. 1954. Modes contractés 'et diffus' de la végétation saharienne. In *Biology of Deserts*, Cloudsley-Thompson JL (ed.). Institute of Biology: London; 35–44.
- Montecinos A, Díaz A, Aceituno P. 2000. Seasonal diagnostic and predictability of rainfall in subtropical South America based on tropical Pacific SST. *Journal of Climate* **13**: 746–758.
- Moreno PI. 1997. Vegetation and climate near Lago Llanquihue in the Chilean Lake District between 20200 and 9500 ¹⁴C yr BP. *Journal of Quaternary Science* **12**: 485–500.
- Moreno PI, Villagrán C, Marquet PA, Marshall LG. 1994. Quaternary paleobiogeography of northern and central Chile. *Revista Chilena de Historia Natural* **67**: 487–502.
- Moreno PI, Lowell TV, Jacobson GL, Denton GH. 1999. Abrupt vegetation and climate changes during the Last Glacial Maximum and Last Termination in the Chilean Lake District: a case study from Canal de la Puntilla (41° S). *Geografiska Annaler* **81**: 285–311.
- Pearson S, Betancourt JL. 2002. Understanding arid environments using fossil rodent middens. *Journal of Arid Environments* **50**: 499–511.
- Rech JA, Quade J, Betancourt JL. 2002. Late Quaternary paleohydrology of the central Atacama Desert. *Geological Society of America Bulletin* **114**: 334–348.
- Rutllant J, Fuenzalida H. 1991. Synoptic aspects of the central Chile rainfall variability associated with the southern Oscillation. *International Journal of Climatology* **11**: 63–76.
- Schmithusen J. 1956. Die räumliche Ordnung der Chilenischen Vegetation. *Bonner Geographische Abhandlungen* **17**: 1–86.
- Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac G, van der Plicht J. 1998. INTCAL98 Radiocarbon age calibration 24,000–0 cal. BP. *Radiocarbon* **40**: 1041–1083.
- Sylvestre F, Servant M, Servant-Vildary S, Causse C, Fournier M, Ybert JP. 1999. Lake-level chronology on the Southern Bolivian Altiplano (18°–23° S) during late-glacial time and the early Holocene. *Quaternary Research* **51**: 54–66.
- Thompson RS. 1985. Palynology and *Neotoma* middens. *American Association of Stratigraphic Palynology Contribution Series* **16**: 89–112.
- Van Devender TR. 1988. Discussion to 'Pollen in packrat (*Neotoma*) middens: pollen transport and the relationship of pollen to vegetation' by Davis, O.K. & R.S. Anderson. *Palynology* **12**: 221–229.
- Veit H. 1996. Southern westerlies during the Holocene deduced from geomorphological and pedological studies in the Norte Chico, Northern Chile (27–33°S). *Palaeogeography, Palaeoclimatology, Palaeoecology* **123**: 107–119.
- Villagrán C. 1988a. Expansion of Magellanic moorland during the late Pleistocene: palynological evidence from northern Isla de Chiloe, Chile. *Quaternary Research* **30**: 304–314.
- Villagrán C. 1988b. Late Quaternary vegetation of southern Isla Grande de Chiloe, Chile. *Quaternary Research* **29**: 294–306.
- Villagrán C, Hinojosa LF. 1997. Historia de los bosques del sur de Sudamérica II: análisis biogeográfico. *Revista Chilena de Historia Natural* **70**: 241–267.
- Villagrán C, Kalin-Arroyo MT, Marticorena C. 1983. Efectos de la desertización en la distribución de la flora andina de Chile. *Revista Chilena de Historia Natural* **56**: 137–157.
- Villagrán C, León A, Roig FA. 2004. Paleodistribución del alerce y ciprés de las Guaitecas durante períodos interestadiales de la Glaciación Llanquihue: provincias de Llanquihue y Chiloé, Región de Los Lagos, Chile. *Revista Geológica de Chile* **31**: 133–151.
- Vuille M, Ammann C. 1997. Regional snowfall patterns in the High, Arid Andes. *Climatic Change* **36**: 413–423.
- Vuille M, Keimig F. 2004. Interannual variability of summertime convective cloudiness and precipitation in the central Andes derived from ISCCP-B3 data. *Journal of Climate* **17**: 3334–3348.
- Wyrwoll K-H, Dong B, Valdes P. 2000. On the position of southern hemisphere westerlies at the Last Glacial Maximum: an outline of AGCM simulation results and evaluation of their implications. *Quaternary Science Reviews* **19**: 881–898.