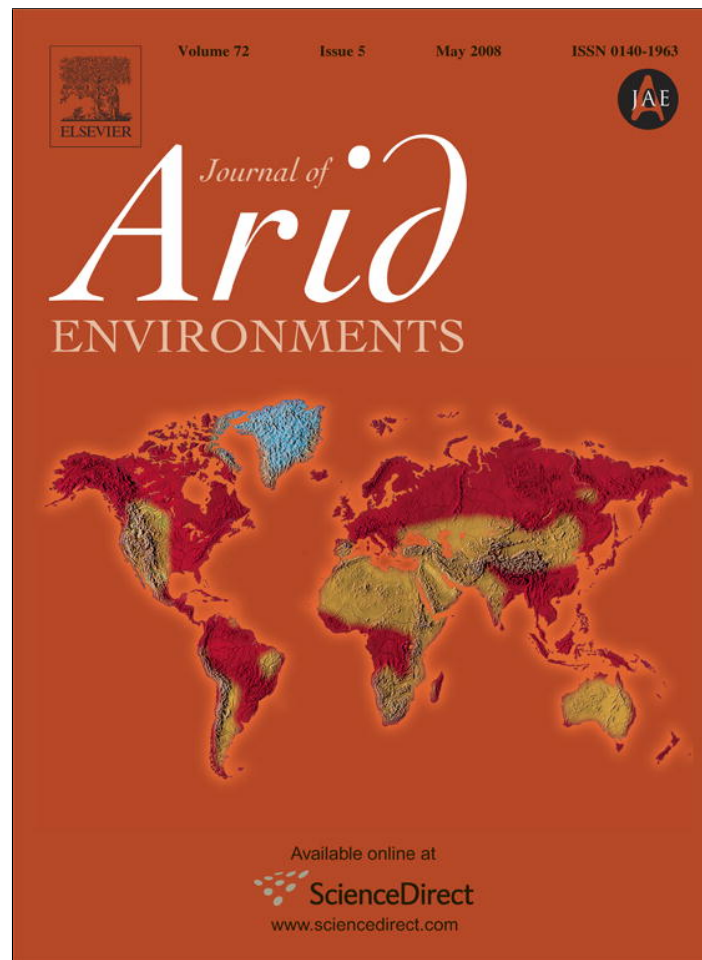


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Late-Holocene fossil rodent middens from the Arica region of northernmost Chile

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Abstract

Identification of >40 taxa of plant macrofossils in 14 rodent (*Abrocoma*) middens collected from 2800 to 3590 m elevation at the latitude of Arica, Chile (18°S) provide snapshots of vegetation in the northernmost Atacama Desert over the past 3000 years. Midden floras show considerable stability throughout the late Holocene, which may be due in part to the broad elevational ranges of many perennial species and midden insensitivity to changes in plant community structure. The greatest variability is found in annuals in the Prepuna, a climatically sensitive zone. This variability, however might also arise from the brevity of midden depositional episodes. As the first midden record from the Arica–Parinacota Region (Chile's northernmost administrative region), this study demonstrates the potential for future midden research in this area.

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1. Introduction

Plant macrofossils preserved in rodent middens have proven a valuable source of late Quaternary paleoecological and paleoclimatological evidence in arid and semi-arid regions of the Western Hemisphere and other parts of the world (Betancourt, 2004; Betancourt and Saavedra, 2002; Betancourt et al., 1990; Pearson and Betancourt, 2002). During the past decade, much of the focus has been on developing the midden record from the Pacific slope of the central Andes (16–26°S) just above hyperarid core of the Atacama Desert in southern Peru and northern Chile (Betancourt et al., 2000; Holmgren et al., 2001; Latorre et al., 2002, 2003, 2005, 2006; Maldonado et al., 2005). These studies have been pivotal in chronicling past pluvial events when plant distributions were displaced up to 1000 m in elevation, with the midden assemblages able to resolve both the seasonality and amount of precipitation. As in North America, hundreds of radiocarbon-dated and

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archived middens from the Atacama are now being mined for a variety of studies (e.g., Kuch et al., 2002). Here, we report on plant macrofossil assemblages spanning the last 3200 yr BP from 14 fossil rodent middens collected in the Andean Precordillera east of Arica, Chile, not far from the Peruvian border. Middens from this region can provide vegetation histories to support interpretation of the rich archeological legacies of the Atacama region.

Rodent middens are deposits of plant materials (seeds, leaves, twigs, bones, pollen, and fecal pellets) encased in crystallized urine, and are abundantly preserved in rock shelters, crevices, and caves in the Atacama Desert. Both Pleistocene and Holocene-aged plant macrofossils are often identifiable at the species level, providing high taxonomic resolution. Rock dwelling rodents typically have very limited foraging ranges so these deposits also represent the surrounding vegetation with a high degree of spatial resolution. A recent taphonomic study of *Abrocoma* middens from northern Chile indicated that no plants from beyond 30 m were found within modern middens (Salinas and Latorre, 2007). Radiocarbon dates from midden plant materials or fecal pellets provide excellent chronological control. However, middens are stratigraphically discontinuous; therefore individual middens represent “snapshots” of floral assemblages that have to be collated to develop local chronologies of vegetation change.

Midden-forming rodents in northern Chile include *Abrocoma cinerea* (Abrocomidae), *Lagidium viscacia* (Chinchillidae), and *Phyllotis* spp. (Cricetidae). Based on fecal pellets, all middens in our study were made by *Abrocoma*, although the diurnal *L. viscacia* was often spotted on rocky hillslopes. *A. cinerea* has a generalist diet (Cortés et al., 2002), and in addition to caching food, these rodents collect plant materials for nest and den construction, resulting in midden assemblages that are representative of hillslope vegetation within the foraging ranges of the animals. Although the surrounding vegetation is well represented in modern *A. cinerea* middens, dietary selectivity may increase in more productive environments (Salinas and Latorre, 2007) such as in our study area, potentially introducing bias. A bias in plant abundance in the midden record may also result from variations in the length of depositional episodes and a tendency for rodents to collect plants growing nearest to the midden.

2. Study area

2.1. Geology and climate

The study area is located on the Pacific slope of the Cordillera Occidental of the Andes between 2800 and 3590 m elevation (Fig. 1). This slope consists primarily of Cretaceous–Tertiary volcanic rocks, especially ignimbrites. Ignimbrites form from very mobile volcanic flows consisting of ash particles and heated volcanic gases, with some of the most massive deposits in northern Chile covering 1000–3000 km³ (Seyfried et al., 1999). Abundant caves and rockshelters within the ignimbrites provide locations suitable for midden preservation throughout the study area. Tertiary eolian and alluvial sediments fill the valleys to the west. Deep, steep-walled valleys oriented east–west surrounding Arica are a result of tectonic destabilization and the collapse of massive packets of sediments (Seyfried et al., 1999). Several volcanoes with peaks between 5000 and 6000 m punctuate the landscape.

The climate of the study area is hyperarid due to a combination of factors including location beneath the South Pacific Anticyclone high-pressure zone, the cold upwelling Peruvian Current offshore that creates a temperature inversion and inhibits convection, and the rainshadow effect of the Andes blocking moisture from the Amazon. The scarce precipitation that does occur comes from three primary sources. At elevations below ~1000 m thick fog develops during the winter due to a temperature inversion off the Pacific coast. Where it intersects the steep coastal slopes it provides sufficient moisture to support “lomas” vegetation. These fog-zone communities exist as bands of vegetation surrounded by hyperarid habitat and consist of highly variable mixtures of annuals, short-lived perennials, succulents, and woody scrub vegetation, often with high levels of endemism (Rundel et al., 1991). During summer months, the South America Summer Monsoon (SASM) brings convective moisture across the Andes as heating occurs over the Amazon Basin. Because of the strong rainshadow effect of the Andes, much of the moisture from summer monsoon storms that cross the Andes falls at high elevations and rarely reaches the coast (Houston and Hartley, 2003). Interannual summer precipitation variability is primarily influenced by El Niño–Southern Oscillation (ENSO) and the strength and position of

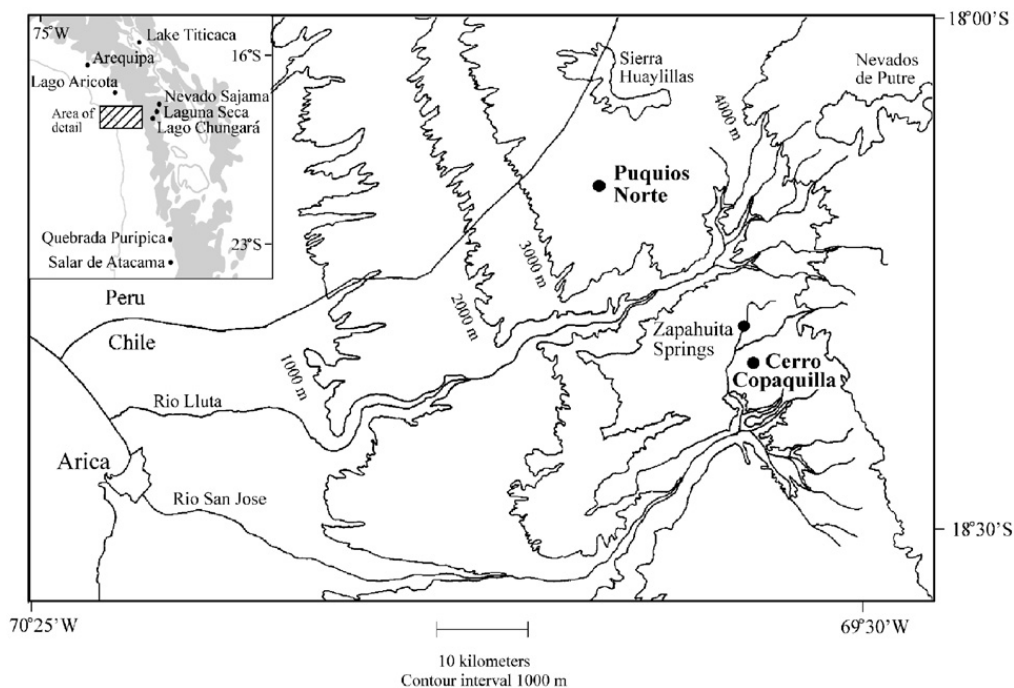


Fig. 1. Map of study area in northernmost Chile showing the location of sites mentioned in the text. Midden sites at Puquios Norte and Cerro Copaquilla are indicated in bold.

the Bolivian High and South Atlantic convergence zone, with wetter conditions association with La Niña events and drier ones with El Niños (Garreaud et al., 2003; Lenters and Cook, 1999; Vuille and Keimig, 2004; Zhou and Lau, 1998). Further to the south ($>25^{\circ}\text{S}$), rainfall occurs primarily during winter when the South Pacific Anticyclone weakens and allows polar fronts and cut-off low pressure cells to travel northward (Miller, 1976). On rare occasions, these cells penetrate as far north as the study area to generate winter precipitation (Vuille, 1999).

Arica, located on the coast at 5 m elevation, receives less than 1 mm of precipitation/year. For the period of record from 1931 to 1989, most of the scant moisture fell during winter months (June–September) in years with strong El Niño events: 1940–1941, 1957–1958, 1972–1973, and 1982–1983 (Ortlieb and Macharé, 1993), with smaller amounts occurring in summer months (December–February). At the higher elevations of our study area, SASM precipitation dominates and contributes 10's to 100's of millimeters of precipitation per year, depending on elevation. Murmuntani, located at 3280 m and less than 20 km northeast of our site at Cerro Copaquilla, receives an annual average of 156 mm of precipitation, while Parinacota Volcano at 4395 m receives 372 mm (Arroyo et al., 1988). Because vegetation in the study area is primarily limited by the amount of summer rainfall, which varies as a function of rainout with elevation and distance from the crest of the Andes, any displacement of species up or downslope recorded in rodent middens should reflect changes in the amount of precipitation received.

2.2. Vegetation

Vegetation in northern Chile can be divided into several vegetation bands. Vegetation classification and characteristic species are based on previous studies (Villagrán et al., 1982, 1983) and our own observations. A table of plant taxa including family, growth form, and common name is available in Appendix A, electronic version only. With the exception of occasional herbaceous lomas vegetation below ~ 1000 m, the Cordillera Occidental below ~ 2700 m consists of “Absolute Desert” where plants are absent from the landscape. Above ~ 2700 m, Absolute Desert gives way to the Prepuna located in the Andean Precordillera and consisting of widely spaced xerophytic plants characterized by the shrubs *Atriplex imbricata*, *Ambrosia artemisioides*, the cactus *Browningia*, and the annuals *Calandrinia*, *Lepidium*, and *Cistanthe*. The Tolar, or Puna, between ~ 3400

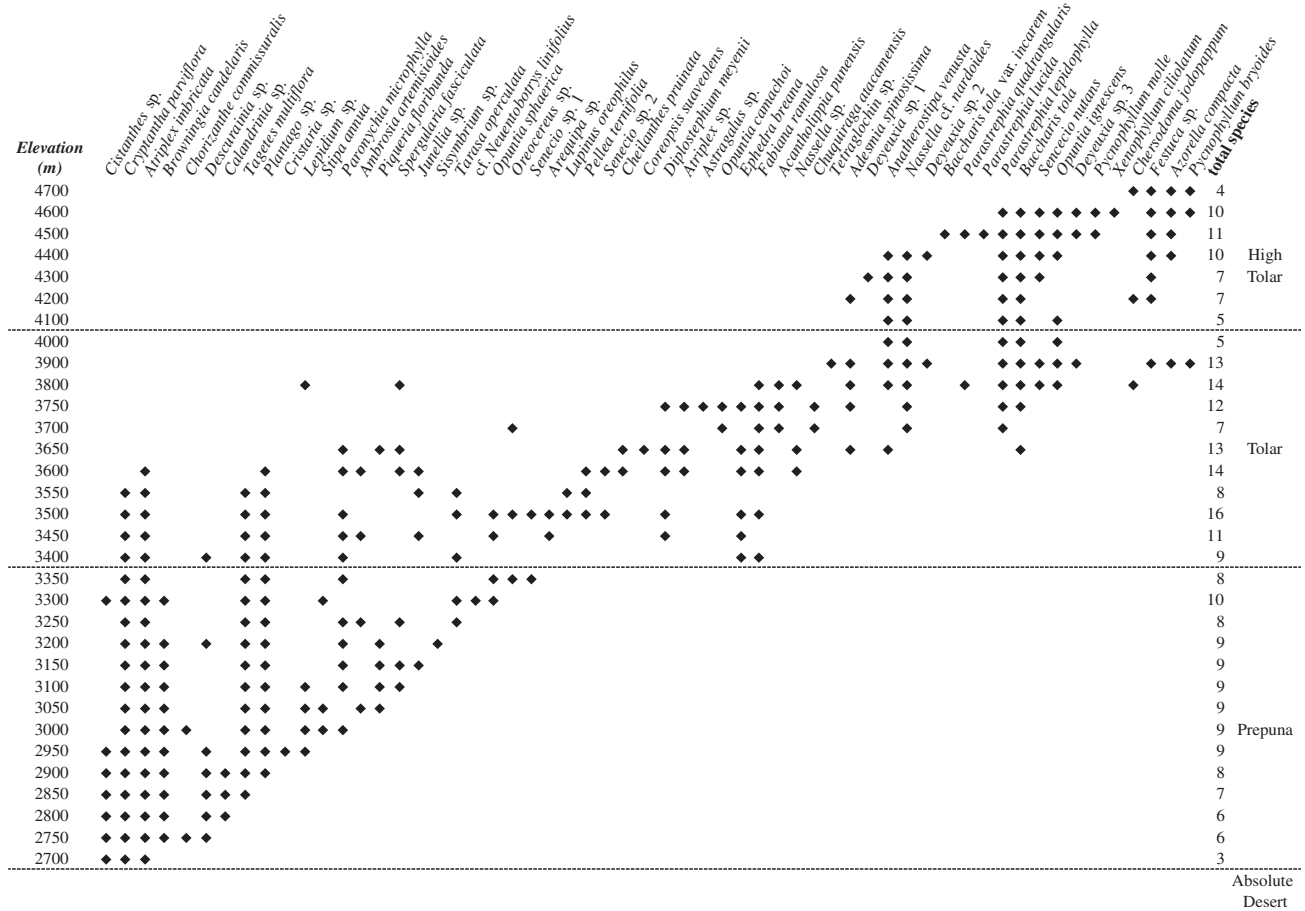


Fig. 2. Vegetation transect from 2700 to 4700 m along the northern oil pipeline road showing the change in plant species with elevation.

and 4000 m is a diverse shrub belt characterized by scrub-type vegetation including *Ephedra breana*, *Fabiana ramulosa*, *Diplostegium*, and *Baccharis tola*. The transitional zone between the Tolar and High Tolar includes tussock grasses and cushion plants, but is dominated by shrubs of the Asteraceae family (*Baccharis*, *Chuquiraga*, and *Parastrephia*). The High Tolar above ~4000 m is dominated by the tussock grasses *Festuca* and *Deyouxia* and the cushion plants *Azorella compacta* and *Pycnophyllum bryoides*. A pronounced vegetation gradient with elevation is evident in the transect we measured from 2700 to 4700 m along the northern oil pipeline road (Fig. 2).

3. Methods

Nine rodent middens were collected from the Puquios Norte site near the Puquios Railroad Station (3443–3589 m) and five from Cerro Copaquilla (2950–3140 m) southeast of Zapahuira (Fig. 1), and represent the first midden records from the Arica–Parinacota Region of northernmost Chile. The elevation of Cerro Copaquilla is located within the Prepuna zone and the elevation of Puquios Norte corresponds to the transition between the Prepuna and Tolar zones. Middens were processed and analyzed according to well-established procedures (Spaulding et al., 1990). In the laboratory, middens were examined for stratigraphic discontinuities and separated into discrete units if necessary, the outer weathering rind removed with a chisel, and the samples placed into buckets of water to dissolve the crystallized rodent urine (ambrat) and to release midden materials. After wet screening and oven drying, sample weights ranged from ~56 to 258 g. Dry midden material was screened through 2 mm (No. 10) and 1 mm (No. 18) sieves to separate size classes and facilitate sorting of plant remains. The entire 2-mm portion and a 1-g subsample from the 1-mm portion were sorted for plant macrofossils and used to assign relative abundances. All remaining material from the 1-mm fraction was also examined for rare types. Macrofossil abundances were quantified using a relative abundance scale of 1–5,

where 0 = 0 fragments, 1 = 1 fragment, 2 = 2–25, 2.5 = 26–50, 3 = 51–75, 3.5 = 76–100, 4 = 101–150, 4.5 = 151–200, and 5 ≥ 200 fragments. Fragments included any identifiable plant part, whether entire or not. Plant taxa were identified based on comparison with modern reference materials including field collections and herbarium specimens. Radiocarbon analyses were done by Geochron Laboratories in Billerica, MA and the dates calibrated using the CALIB 4.4 Intcal04 curve (Stuiver and Reimer, 1993). All values within the text are reported as the midpoint of the calibrated 2σ age ranges (Table 1) to facilitate comparison with other records.

4. Results and discussion

The temporal coverage of the 14 middens is uneven, probably due to the limited number of samples (Table 1). The oldest midden was dated to 3180 yr BP and the next oldest midden does not occur until 1410 yr BP. There is, however, relatively good coverage for the last 1410 years. Given the prevalence of middens > 10,000 yr old in the central and southern Atacama (Latorre et al., 2002, 2003, 2006; Maldonado et al., 2005), we were surprised by the lack of older middens at the sites that we sampled in the Arica region. If there is actually a physical reason for this, it may have to do with higher relative humidity, either in general or episodically, which would prevent or reverse crystallization of rodent urine. Discovery of older middens may require more intensive survey than was feasible in the present study.

Macrofossils from more than 40 taxa in 19 families were identified to genus or species. The relative abundances of select taxa through time are plotted in Fig. 3. The midden record is characterized by the apparent stability of many species. Both modern and past vegetation assemblages contain a mix of Prepuna and Tolar species with a small number of plants from the Tolar–High Tolar transition zone. It is apparent from our transect (Fig. 2) that many of the stable elements have broad elevational ranges and occur across vegetation zones. Species with large elevational ranges may not be sensitive to small variations in precipitation. The persistence of species with more restricted elevational ranges such as *Tarasa operculata*, *Sisymbrium*, *Opuntia sphaerica*, and *Coreopsis suaveolens*, however, suggests that the amount of precipitation received in the study area during the late Holocene may have been relatively stable.

The species that exhibit the greatest variability in our record are annuals found in the Prepuna zone. These include *Cardionema* cf. *andina*, *Cistanthe*, *Cristaria*, *Lepidium*, *Nolana*, and *Parietaria debilis*. Because SASM precipitation rains out at higher elevations, the lower Prepuna zone tends to receive smaller amounts and less reliable precipitation. Adequate germination conditions are met only in occasional years, so the greater temporal variability of annuals, compared to perennials that can establish in good years and persist through less favorable ones, is not surprising. On the other hand, annuals can probably establish in Absolute Desert uninhabitable by perennials. The fringe of vegetation near Absolute Desert is transient through time due to occasional “invasions” by annuals into Absolute Desert. This is possible due to the longer viability of annual seed banks. Arroyo et al. (1988) have noted that the percentage of annuals between 18 and 19°S is greatest at lower elevations (2000–3000 m), although annual cover fluctuates widely between wet and dry years. In addition, annuals require warmer conditions, which may also explain their greater abundance at lower elevations. These factors may likewise be responsible for the patchy record of annual grasses, which are more common at the lower elevation site of Cerro Copaquilla. The greatest number of grasses and Prepuna annuals are present at 800 and 390 yr BP at Copaquilla and 3180, 1410, 590, and 250 yr BP at Puquios Norte, possibly denoting periods of increased precipitation. Replication of this pattern from more middens will help verify whether the greater number of annuals during these periods does indeed reflect increased precipitation.

Mid- to late-Holocene climate proxy records show conflicting precipitation levels between the Altiplano and the Pacific slope of the Andes. After ~3500 yr BP lake levels (Abbott et al., 2003; Baker et al., 2001) and ice cores (Thompson et al., 1998) suggest the onset of wetter conditions on the Altiplano. Superimposed on this trend are periods of lowered lake levels from 3200 to 2800, 2400 to 2200, 1700 to 1500, and 900 to 600 yr BP (Abbott et al., 1997, 2003). Mourguiart et al. (1998) see a similar rise in Lake Titicaca water levels after ~4200 yr BP, a dry phase around 2200 yr BP, and a final wet phase after 600 yr BP. Although Lake Titicaca records indicate increased moisture after ~600 yr BP, a core from Lago Chungará (18°15'S) shows this was interrupted by periods of increased salinity and lower water levels between 1880–1905 and 1935–1950 AD (Valero-Garcés et al., 2003). At Laguna Seca (18°11'S) an increase in herbaceous pollen suggests drier conditions beginning ~4000–3000 yr BP, although this change in vegetation may result from the onset of

Table 1
Radiocarbon dates and site locations of rodent middens

Midden designation	Material dated	¹⁴ C Age (yr BP)	Lab code	δ ¹³ C (‰)	Calibrated (2σ) age range (yr BP)	Midpoint of calibrated age range	Latitude (°S)	Longitude (°W)	Elevation (m)	Slope aspect
Puquios Norte 524A	Fecal pellets	3050 ± 60	GX-27394	−24.1	3000–3355	3180	S18°12.068'	W69°46.312'	3589	WNW
Puquios Norte 526	Fecal pellets	1160 ± 70	GX-27355	−23.5	851–1256	1050	S18°12.061'	W69°46.363'	3576	ESE
Puquios Norte 528	Fecal pellets	1550 ± 60	GX-27393	−23.8	1302–1522	1410	S18°12.163'	W69°46.450'	3527	SE
Puquios Norte 530A	Fecal pellets	640 ± 60	GX-27356	−23.6	521–662	590	S18°12.136'	W69°46.488'	3545	ESE
Puquios Norte 533	Fecal pellets	310 ± 80	GX-27446	−23.9	0–499	250	S18°12.438'	W69°46.601'	3498	SE
Puquios Norte 507	Fecal pellets	800 ± 60	GX-27391	−23.6	564–790	680	S18°12.518'	W69°46.585'	3500	NW
Puquios Norte 510C	Fecal pellets	1310 ± 80	GX-27396	−23.4	976–1309	1140	S18°12.609'	W69°46.824'	3443	ESE
Puquios Norte 534B	Fecal pellets	1340 ± 60	GX-27354	−23.8	1067–1306	1190	S18°12.577'	W69°46.820'	3453	E
Puquios Norte 574	Fecal pellets	160 ± 50	GX-27359	−24.1	0–279	140	S18°12.345'	W69°42.751'	3450	S
Copaquilla 519B	Fecal pellets	340 ± 60	GX-27392	−23.6	153–496	330	S18°23.674'	W69°38.037'	2950	SE
Copaquilla 545B	Fecal pellets	920 ± 40	GX-27447	−19.6	687–905	800	S18°23.686'	W69°39.090'	2969	N
Copaquilla 564	Fecal pellets	360 ± 60	GX-27358	−23.6	283–499	390	S18°23.664'	W69°39.113'	2960	SE
Copaquilla 553	Fecal pellets	530 ± 60	GX-27448	−23.2	334–632	480	S18°25.176'	W69°38.904'	3100	SSE
Copaquilla 568	Fecal pellets	410 ± 80	GX-27395	−20.9	283–538	410	S18°25.378'	W69°39.144'	3140	N

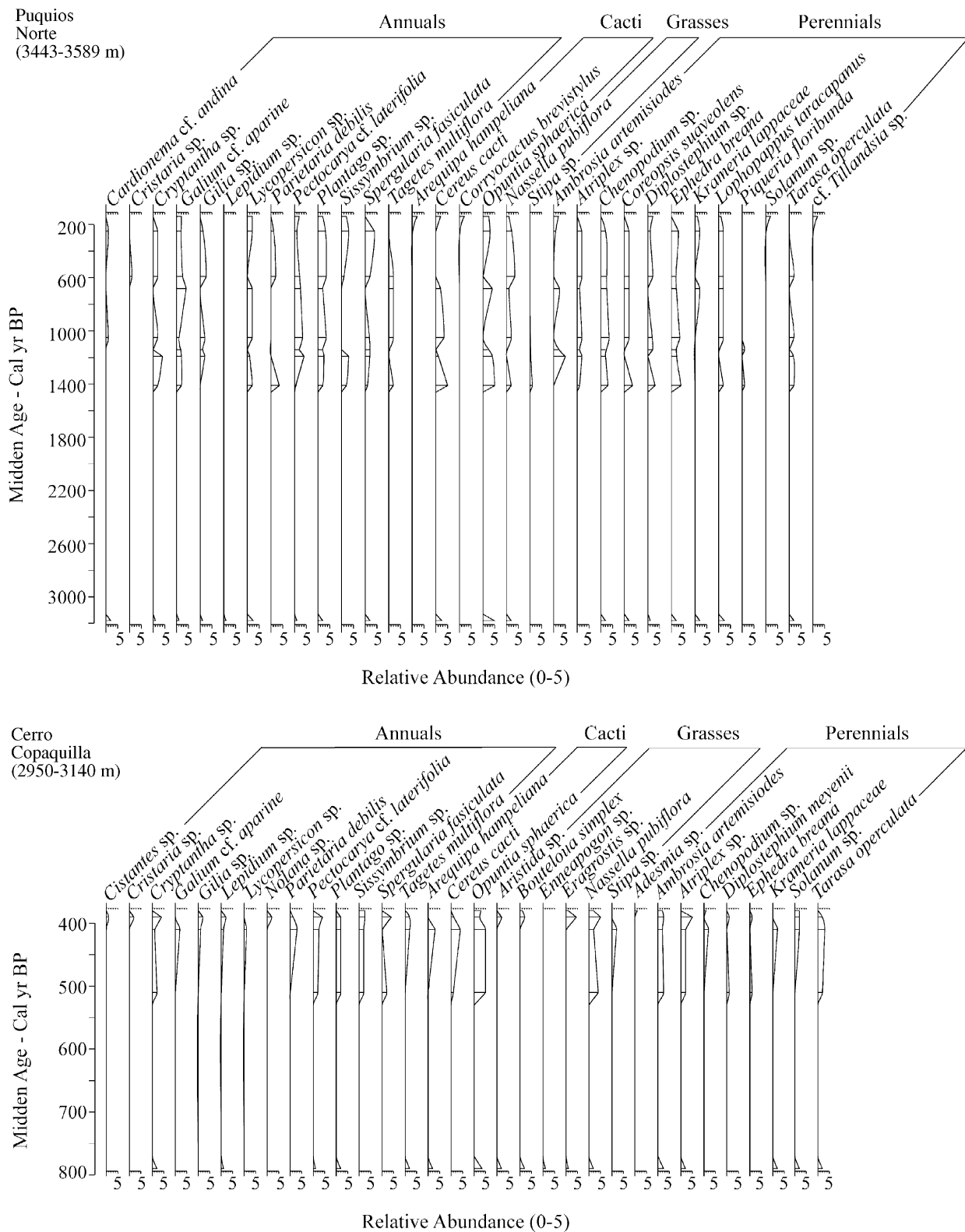


Fig. 3. Plant macrofossil abundance through time for select species from Puquios Norte (top graph) and Cerro Copaquilla (bottom graph). Note the change in scale along age axis for the two sites.

camelid pastoralism rather than changes in moisture supply (Baied and Wheeler, 1993). Clearly, there is not enough agreement among records to present an unified picture of late-Holocene climate on the Altiplano.

Unlike the Altiplano, records from the Pacific slope of the Andes indicate generally drier conditions during the late Holocene. Wetter periods superimposed on this drying trend are often out of phase with Altiplano records. Wetland deposits from Zapahuira Springs (18–19°S), located in close proximity to our study site, dating from 3100 to 1300 and 1200 to 400 yr BP and springs at Quebrada Puripica (23°S) dating from 2600 to 1300 yr BP indicate higher water table levels during times of lowered water levels in Altiplano lakes (Rech, 2001; Rech et al., 2003). Middens from 22 to 23°S near the Salar de Atacama also suggest wet conditions from 3490 to 2320 yr BP (Latorre et al., 2006), 1800 to 1200 yr BP (Latorre et al., 2003), and ~800 yr BP (Latorre et al., 2006; Maldonado et al., 2005). In Peru, Lago Aricota (17°22'S) likewise developed high stands at 1700 and 1300 yr BP (Placzek et al., 2001).

Our midden record, which is admittedly sparse, indicates vegetation from the Arica area has been relatively stable for at least 1410 yr BP, and possibly for as long as 3180 yr BP. The trends towards drier conditions noted in other records from the Pacific slope of the Andes and fluctuations between wetter and drier conditions seen in records elsewhere in the region are not evident in our record. Instead, the arid Pacific slope of the Andes at the latitude of Arica supported a harsh but stable environment occupied by xerophytic shrubs, annuals, and cacti. However, as stated previously, this apparent stability may simply be a reflection of the broad elevational ranges of several perennial species present in the record. Also, because midden assemblages are subject to bias due to filtering by rodents, macrofossils species presence or absence data are generally more reliable than macrofossil relative abundances and changes in plant community structure (species abundances) may or may not be recorded in the midden record (Holmgren et al., 2001). In any case, the cause of discrepancies in records from the Altiplano and Pacific slope of the Andes remains unresolved. It is possible that these discrepancies are due to variations in temporal resolution, response time, and/or record sensitivity. They may also result from the geographical complexity of the regional climate and diverse controls on interannual variability in northern Chile (Vuille and Keimig, 2004).

Despite some uncertainty in the climatic interpretation possible from this record, our study clearly demonstrates the potential for future midden studies in northernmost Chile. As in the central Atacama Desert, rodent middens in northernmost Chile represent a key resource for reconstructing late Quaternary vegetation and evaluating climatic evidence derived from paleohydrologic records. In order to increase the scope of inference, we suggest that larger numbers of middens will be needed to both increase temporal coverage and resolution, while allowing for greater replication of reconstructed vegetation assemblages and patterns. Finally, identification of more sensitive areas for prospecting is needed. Whereas many middens have been collected near the lower limits of vascular plants in the central and southern Atacama, rocky areas suitable for midden preservation in the Arica area occur at higher elevations where the vegetation may be less sensitive to precipitation variability and perhaps more sensitive to past variations in temperature. Continued exploration will no doubt lead to more favorable collection locales in northernmost Chile.

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Appendix A. Supplementary Material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jaridenv.2007.09.003](https://doi.org/10.1016/j.jaridenv.2007.09.003).

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