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Rodent middens reveal episodic, long-distance plant colonizations across the hyperarid Atacama Desert over the last 34,000 years

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ABSTRACT

Aim To document the impact of late Quaternary pluvial events on plant movements between the coast and the Andes across the Atacama Desert, northern Chile.

Location Sites are located along the lower and upper fringes of absolute desert (1100–2800 m a.s.l.), between the western slope of the Andes and the Coastal Ranges of northern Chile (24–26° S).

Methods We collected and individually radiocarbon dated 21 rodent middens. Plant macrofossils (fruits, seeds, flowers and leaves) were identified and pollen content analysed. Midden assemblages afford brief snapshots of local plant communities that existed within the rodents' limited foraging range during the several years to decades that it took the midden to accumulate. These assemblages were then compared with modern floras to determine the presence of extralocal species and species provenance.

Results Five middens span the last glacial period (34–21 ka) and three middens are from the last glacial–interglacial transition (19–11 ka). The remaining 13 middens span the last 7000 years. Coastal hyperarid sites exhibit low taxonomic richness in middens at 19.3, 1.1, 1.0, 0.9, 0.5 ka and a modern sample. Middens are also dominated by the same plants that occur today. In contrast, middens dated to 28.1, 21.3, 17.3, 3.7 and 0.5 ka contain more species, including Andean extralocals. Precordillera middens (c. 2700 m) show a prominent increase in plant macrofossil richness, along with the appearance of Andean extralocals and sedges at 34.5 and 18.9 ka. Six younger middens dated to 6.1–0.1 ka are similar to the modern local vegetation.

Main conclusions Increased species richness and Andean extralocal plants occurred along the current lower fringes of absolute desert during the last glacial–interglacial transition and late Holocene. The absence of soil carbonates indicates the persistence of absolute desert throughout the Quaternary. Colonization by Andean plants could have been accomplished through long-distance seed dispersal either by animals or floods that originated in the Andes. We postulate that dispersal would have been most frequent during regional pluvial events and associated increases in groundwater levels, forming local wetlands in the absolute desert, and generating large floods capable of crossing the Central Depression.

Keywords

Abrocoma, aridland palaeoecology, Atacama Desert, fog oases, hyperarid environments, late Quaternary, Lomas vegetation, *Phyllotis*, rodent middens.

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INTRODUCTION

Supported by semi-permanent fog bank and separated from the Andes by a forbidding stretch of absolute desert, the coastal *Lomas* are among the most intriguing plant formations of the Atacama Desert, if not the world (Rundel *et al.*, 1991, 1996; Squeo *et al.*, 1998). The *Lomas* formation owes its great diversity and high levels of endemism (c. 50%) to 'splendid isolation' by the Pacific to the west and the hyperarid core of the Atacama to the east, the latter originating in the middle to late Miocene (Houston, 2006a; Rech *et al.*, 2006, 2010). Many endemics in the *Lomas* formations represent allo-disjuncts from ancestral, congeneric stocks or auto-disjuncts originating from extant, conspecific populations in the Andes (Dillon, 2005; Luebert *et al.*, 2009). Much recent molecular work on different *Lomas* plant families shows that divergence probably dates back to the Pliocene (Gengler-Nowak, 2002; Dillon *et al.*, 2009; Luebert *et al.*, 2009). Yet divergence may have also occurred at a later date. For example, phylogenetic data indicate that the Malesherbiaceae diverged well before the late Pleistocene. The divergence of Malesherbiaceae subgenera, however, has been postulated to have happened during the Pleistocene–early Holocene, when increasing aridity presumably fragmented more continuous distributions into distinct and genetically isolated populations (Gengler-Nowak, 2002). Until now, palaeorecords of climate or vegetation change have been lacking to test this hypothesis.

Very little is known about late Quaternary climate in the coastal Atacama Desert except for a prominent increase of c. 5–8 °C in sea surface temperatures (SST) during the last glacial–interglacial transition (Kim *et al.*, 2002; Mohtadi *et al.*, 2004; Latorre *et al.*, 2007; Marchant *et al.*, 2007). This warming of coastal waters was coeval with rising lake levels in the central Andes and Bolivian Altiplano (Grosjean *et al.*, 1995; Baker *et al.*, 2001; Placzek *et al.*, 2006, 2009; Hillyer *et al.*, 2009) and groundwater displacements on the Pacific slope of the Andes and the western Precordillera (Rech *et al.*, 2002; Nester *et al.*, 2007; Quade *et al.*, 2008).

Previous work with fossil rodent middens in the central Atacama (22–24° S; Betancourt *et al.*, 2000; Latorre *et al.*, 2002, 2003, 2006; Maldonado *et al.*, 2005) points to a major pluvial event during the last glacial–interglacial transition, beginning c. 17.5 ka, which then lasted for another 7000 years. These records document the downslope migration (by up to 1000 m of elevation) of many species of grasses and shrubs found exclusively today on the Altiplano (> 3800 m). These plants invaded the species-poor lower vegetation belts (Prepuna, 2600–3300 m) increasing the number of species present five-fold and probably contracting the upper extent of the absolute desert (Latorre *et al.*, 2002, 2005; Maldonado *et al.*, 2005).

Augmented rainfall at high elevations generated perennial riverflow in areas that today are barren of vegetation and surface water (Nester *et al.*, 2007). Indeed, palaeobotanical and geomorphological evidence indicates that significant portions of the hyperarid core of the northern Atacama Desert

(> 400 km from our study area) exhibited perennial surface flow from 17.8 to 13.8 ka and then at 11.8 ka (Nester *et al.*, 2007). The biogeographical and evolutionary consequences for plant and animal populations of these well-dated events have been little explored in the lower desert (< 2000 m), including their potential role in the evolution of *Lomas* plant communities.

We undertook a midden survey in what is today absolute desert, a vast, mostly rainless and plantless region c. 100 km wide and 1200 km long in northern Chile (Arroyo *et al.*, 1988; Marquet *et al.*, 1998) (Fig. 1). Our survey between 1200 and 2700 m elevation and 24 and 26° S latitude yielded 21 middens made by chinchilla rats (*Abrocoma*) or leaf-eared mice (*Phyllotis*) and spanning the last 34,000 years, with the oldest middens coming from sites within 50 km of the coast in the lower fringes of absolute desert. Because plants, animals and suitable outcrops for midden preservation are truly sparse in this region, we were fortunate to glean such a long midden record.

Here, we use the plant species composition (especially extralocal species) present in our rodent middens to document changes in bioavailable moisture and evaluate the consequences of these changes in the species composition of absolute desert and coastal *Lomas* plant communities during the late Quaternary. By comparing rodent middens from small mountain ranges in the Central Depression and near the Pacific coast with contemporary ones from the western slope of the Andes and Precordillera we obtain a first approximation of episodic, long-distance colonization events from the Andes to the coast, and for the relative roles of dispersal limitations versus favourable conditions for plant establishment.

Past variations in bioavailable moisture in the lower fringes of absolute desert (c. 1200–1900 m) could be due to a variety of circumstances, including: (1) increases in local rainfall from either winter- or summer-derived sources; (2) increases in local fog intensity at slightly higher elevations (> 1000 m), possibly driven by changes in the inversion layer responsible for the fog bank that maintains the *Lomas*; or (3) extreme rainfall > 3000 m and flash floods that traverse the absolute desert/Central Depression (Houston, 2006a), and/or (4) sustained precipitation increases in the Precordillera and Andes and increased aquifer recharge that produces persistent, elevated groundwater levels just east of the Coastal Range (e.g. Nester *et al.*, 2007).

These different moisture sources are not mutually exclusive, but would yield different outcomes or combinations of outcomes in fossil plant assemblages. For example, variations in coastal fog intensity and extent would enable obligate *Lomas* species to occupy higher elevations than the narrow elevational band where they occur today (200–1200 m, Rundel *et al.*, 1991). With increased local rainfall, we would expect to see an increase in plant species richness at the fringes of the absolute desert (Latorre *et al.*, 2002; Maldonado *et al.*, 2005). With increased frequency of large floods and local wetlands associated with elevated regional groundwater levels, we would expect species with distributions currently in the Andean

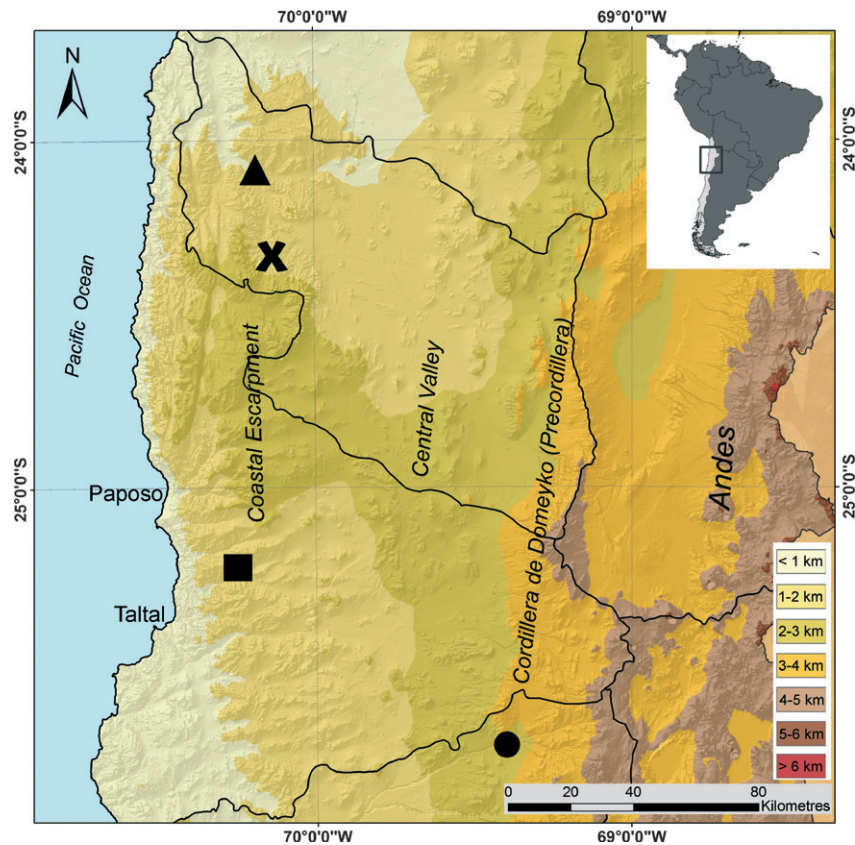


Figure 1 The central–southern Atacama Desert with rodent midden sites: triangle, Barazarte (BZT); cross, Cerro Tres Tetas (CTT); square, Sierra del Buitre (SDB); circle, Quebrada Juncal (QJU). Black lines indicate watersheds.

Precordillera (> 2500 m) to appear in midden records as plants dispersed downslope along intermittent watercourses.

STUDY SITE

Regional context

Straddling the Tropic of Capricorn, the Atacama Desert spans over 10° of latitude from southern Peru into northern Chile and from the Pacific coast to the Andes. The Atacama is probably the world’s driest desert, with recorded precipitation averaging < 1 mm a year at several meteorological stations located in the Central Depression (Houston, 2006b). Multiple exposure age measurements reveal that although some surfaces in the Atacama have remained intact since the early Miocene (Dunai *et al.*, 2005), the onset of hyperaridity probably occurred during the late Miocene coeval with Andean uplift and with an increased intensity of the cold Chile–Peru current (Alpers & Brimhall, 1988; Rech *et al.*, 2006).

Geology and physiography

Our rodent middens were collected along the rare escarpments found along the many east–west oriented valleys that traverse the tectonically active Coastal Range and Andean Cordillera (Fig. 2,

Table 1). At 1200–1900 m a.s.l., middle to upper Jurassic intrusive diorites and granodiorites outcrop at Barazarte (BZT) and Cerro Tres Tetas (CTT), one of the few places where Pleistocene middens were collected in absolute desert settings. Slightly further south, at 1500 m a.s.l. and < 20 km away from the coast, a much older Carboniferous–Permian granite intrusive at Sierra del Buitre (SDB) outcrops along the north flank of the east–west Agua de Cascabel valley. Our final locality, Quebrada Juncal (QJU), is located in the Andean Precordillera or Cordillera Domeyko. Rodent middens were collected along an extensive scarp of Palaeogene volcanoclastic sediments that caps the canyon walls at c. 2750 m of elevation (Fig. 2).

Climate and vegetation

Three major sources of moisture reach the central–southern Atacama Desert. Winter rains during strong negative El Niño–Southern Oscillation (ENSO) years (El Niño) and the year-round presence of fog are important below 900 m along the Coastal Range. Known locally as ‘camanchaca’, this dense coastal fog is prevalent along much of subtropical Chile during late winter to early spring (Rundel & Mahu, 1976; Rundel *et al.*, 1991; Garreaud *et al.*, 2008). In contrast, the western Andean flank and to a lesser extent the Cordillera Domeyko (2000–5000 m) receive sporadic precipitation from either

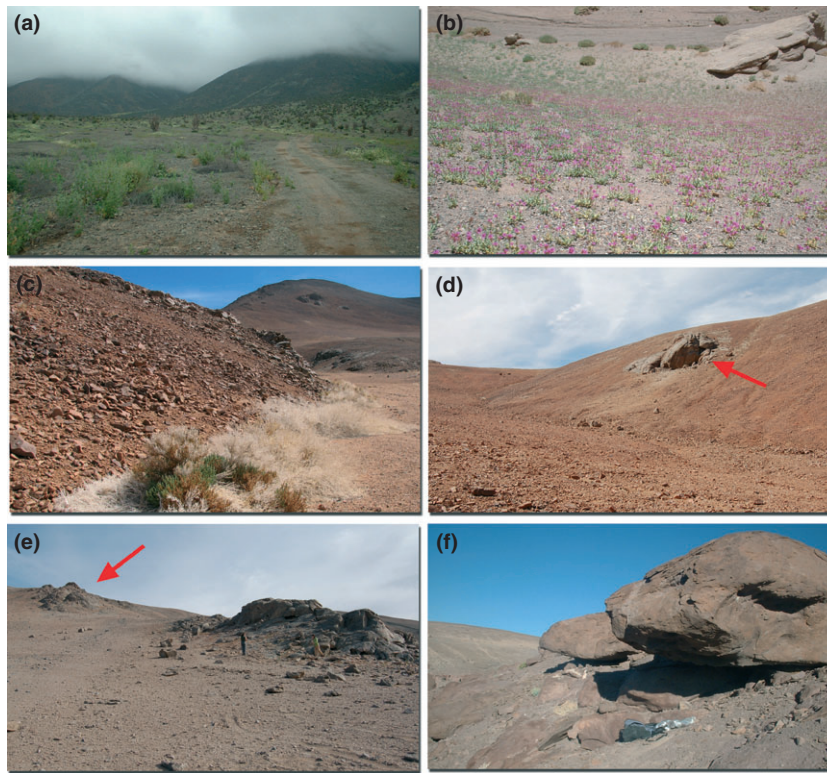


Figure 2 Photographs of rodent midden localities in the central–southern Atacama Desert; arrows indicate where middens were found: (a) Lomas, (b) Precordillera, near Quebrada Juncal (QJU), (c) Sierra del Buitre (SDB), (d) SDB, (e) Barazarte (BZT), (f) Quebrada Juncal (QJU).

Table 1 Local climate parameters estimated for each midden site in the central–southern Atacama Desert.*

Midden site name (Code)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm year ⁻¹)
Barazarte (BZT)	1200	19.5	0.1
Sierra del Buitre (SDB)	1500	16	15
Cerro Tres Tetras (CTT)	1900	15.6	1
Quebrada Juncal (QJU)	2750	8.5	75

*Based on data from the Dirección General de Aguas (see Houston, 2006b).

frontal systems or cut-off lows during winter (Vuille & Ammann, 1997) and convective rainfall associated with the tropical easterlies in summer (Garreaud *et al.*, 2003).

The frequency, intensity and extent of modern day inter-annual precipitation variability in the Atacama Desert are modulated to varying degrees by the ENSO (Garreaud *et al.*, 2003; Houston, 2006b). Positive ENSO anomalies ('La Niña') tend to be associated with increased summer rainfall in the high Andes (Vuille *et al.*, 2000; Garreaud *et al.*, 2003; Vuille & Keimig, 2004) whereas negative ENSO anomalies ('El Niño') are associated with increased winter precipitation along the coast and lower elevations of the Andean flank (Houston, 2006b). Complex interactions can arise as expansions and

contractions of the Hadley circulation cause the summer/winter transition zone to move south or north (Diaz & Bradley, 2004; Houston, 2006b). These modern relationships may also have changed on lengthier time-scales (i.e. centennial, millennial and orbital) as forced by changes in regional insolation (Lamy *et al.*, 2000; Clement *et al.*, 2004).

The relationship between ENSO and coastal fog can be spatially complex. A 10-year study from northern Chile (*c.* 21° S) shows little or no correlation between ENSO and fog extent or intensity, and in fact some of the foggiest years (e.g. 1997) occurred during negative phases of ENSO (Muñoz-Schick *et al.*, 2001; Cereceda *et al.*, 2008). In contrast, a 22-year record of past fog intensity in subtropical Chile (*c.* 30° S) links positive ENSO anomaly phases with high fog years (Garreaud *et al.*, 2008). The intensity and altitude of the thermal inversion that forms over the coastal Pacific as a result of the interaction between large-scale subsidence and the cold northward-flowing Chile–Peru (Humboldt) current is a key synoptic aspect underlying the extent and duration of major advective fog events.

At present, along a west–east oriented axis, three major types of ecosystems occur in the central–southern Atacama (22–27° S) (Fig. 3). The coastal *Lomas* vegetation (200–900 m), the absolute desert (900–3000 m) and the Andean belt (3000–5000 m) (Schmithüsen, 1956; Rundel *et al.*, 1991; Marquet *et al.*, 1998). Many distinct and endemic species of cacti (*Copiapoa*, *Eulychnia*) and shrubs (*Gyptothamnium*,

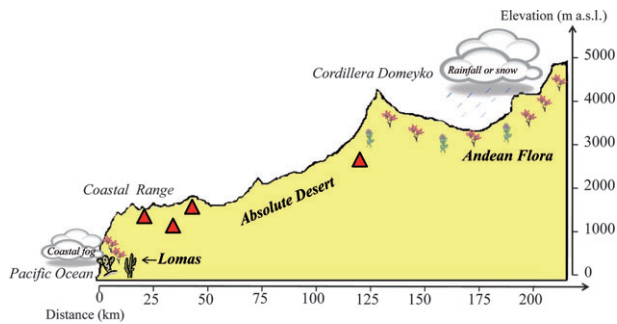


Figure 3 Schematic elevational representation of the different vegetation and geographical zones at 24–25° S, Atacama Desert, Chile. Midden sites (triangles) are indicated for reference.

Euphorbia, *Nolana*, *Heliotropium*, *Sisymbrium*, *Bahia*) occur in the unique *Lomas* floras. The richest and most diverse communities are found in the maximum fog zone between 600 and 800 m (Johnston, 1929; Rundel & Mahu, 1976). A few hardy shrubs and annuals do occur above 1200 m in specific settings such as along roads, on rocky hillslopes and other places where moisture can collect (total cover < 1%), including *Nolana leptophylla*, *Huidobria fruticosa* and *Cistanthe* spp. The absolute desert is completely devoid of vegetation, save for the few 'micro' fog oases (often along rocky outcrops at low elevations), groundwater oases and perennial river valleys. *Nolana*, *Cistanthe*, *Atriplex atacamensis*, *Distichilis spicata* and *Dinemandra ericoides* are among the hardiest plants found in these environments (C.L., pers. obs.; Saiz *et al.*, 2000). Andean vegetation is usually divided into four major belts: Prepuna, Puna (= Tolar), High Andean Steppe and the Subnival. Spanning over 2000 m in elevation, these belts are segregated along major rainfall (which increases with altitude) and temperature gradients. Mean annual precipitation (MAP) averages c. 20 mm at 2600 m and c. 150 mm at 4800 m (data estimated from Houston, 2006b). The Prepuna (2600–3300 m) is a sparsely vegetated shrub belt. Common plants include *Atriplex imbricata* (Chenopodiaceae), *Ephedra multiflora* (Ephedraceae), *Haplopappus rigidus* (Asteraceae) and the annual *Gilia crassifolia* (Polemoniaceae). The more diverse Puna (3300–3800 m) is characterized by *Fabiana* (Solanaceae), *Baccharis* (Asteraceae), *Parastrephia quadrangularis* (Asteraceae), *Acantholippia deserticola* and *Junellia seriphoides* (Verbenaceae). The high Andean Steppe (3800–4500 m) is dominated by tussock grasses *Festuca chrysophylla*, *Deyeuxia cabreriae* and *Nassella nardoides*. A 'Subnival' zone (4500–4800 m) is characterized by small perennial herbs and cushion plants such as *Pycnophyllum bryoides*, *Menonvillea virens*, *Chaetanthera revoluta* and *Urbania pappigera* (Villagrán *et al.*, 1983; Arroyo *et al.*, 1998; Luebert & Gajardo, 2000; Saiz *et al.*, 2000; Latorre *et al.*, 2002).

MATERIALS AND METHODS

We collected, analysed and radiocarbon dated 21 fossil rodent middens from the absolute desert of the central–southern

Atacama Desert (part of Chile's Antofagasta Region). Middens were collected from four different localities at two different elevations. Thirteen middens were collected between 24 and 25.15° S and 1100–2000 m from the lower limit of the absolute desert, above the Coastal Range (SDB, CTT and BZT) (Coastal Range middens) whereas eight middens were collected from QJU along the Andean Precordillera at 2500–3000 m a.s.l. at 25.44° S along the upper limit of the absolute desert (Quebrada Juncal/Precordillera middens) (Figs 1–3, Table 2).

Chronology

Approximately 100 mg of rodent faecal pellets was separated from each midden and radiocarbon dated at the Center for Applied Isotope Studies, University of Georgia, Athens, GA, or at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA (both using AMS ^{14}C). All other conventional radiocarbon dates (3–10 g of pellets) were obtained from Geochron Laboratories, Boston, MA. Dates were calibrated using CALIB 6.0 (Stuiver & Reimer, 1993) and the IntCal09 calibration curve (Reimer *et al.*, 2009). All ages are reported in ka (thousands of calibrated years before present – defined as AD 1950).

Plant macro- and microfossil analyses

Middens were processed following previously described procedures (Betancourt *et al.*, 2000; Betancourt & Saavedra, 2002; Latorre *et al.*, 2002). Fruits, seeds, flowers and leaves (plant macrofossils, Fig. 4) were quantified and identified to the highest possible taxonomic resolution by comparison with a reference collection housed at the Laboratorio de Paleoecología (Departamento de Ecología, P. Universidad Católica de Chile, Santiago) and the plants collected at the sites during midden field sampling. Taxa present in each midden were added up (total richness) and abundance was quantified through the use of a relative abundance index (where 0 is absent and 5 is dominant) (Spaulding *et al.*, 1990).

Seven middens from Quebrada Juncal along with 11 middens from the Coastal Range were analysed for pollen on previously separated indurated voucher samples. Extraction was done on the midden urine matrix (excluding faeces) using standard techniques (Faegri & Iversen, 1989) including a KOH wash, acetolysis, followed by HF then ultrasonication to concentrate grains. General pollen preservation in middens is usually outstanding and they have been shown to be good environmental indicators in the arid zones of Chile (Maldonado *et al.*, 2005). A reference pollen archive and literature (Heusser, 1983) were used to identify fossil pollen.

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. In addition, we used an unconstrained UPGMA (unweighted pair-group method

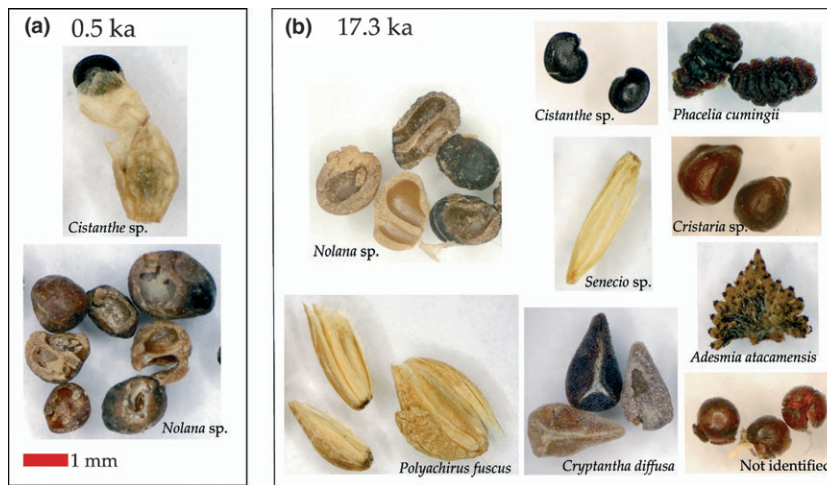


Figure 4 Remarkable preservation of plant macrofossils identified from two middens separated by almost 17,000 years collected at the same site (Sierra del Buitre, SDB) along the Coastal Range: (a) 0.5 ka, (b) 17.3 ka. This preservation is typical of rodent midden plant material and can lead to records with very high taxonomic resolution.

Table 2 Locality information and radiocarbon dates for the 21 middens used in this study.

Midden code	Lab code	Latitude S	Longitude W	Elevation (m)	Age (^{14}C yr BP)	Midden age (ka)†	Agent	Number of taxa
<i>Coastal escarpment</i>								
SDB 113-E		25°13.823'	70°14.451'	1550	Not dated	Modern	<i>Abrocoma</i>	4
SDB 145-C	CAMS-133245	25°13.644'	70°15.099'	1650	385 ± 35	0.5 (0.33–0.50)	<i>Abrocoma</i>	6
SDB 149*	AA69848	25°13.677'	70°15.113'	1644	469 ± 31	0.5 (0.50–0.53)	<i>Abrocoma</i>	2
SDB 113-D	CAMS-133247	25°13.822'	70°14.450'	1550	945 ± 35	0.9 (0.80–0.92)	<i>Abrocoma</i>	4
SDB 147*	AA69847	25°13.915'	70°14.671'	1518	1087 ± 43	1 (0.96–1.05)	<i>Abrocoma</i>	3
SDB 145-B	AA69846	25°13.644'	70°15.099'	1650	1204 ± 45	1.1 (1.06–1.18)	<i>Abrocoma</i>	2
SDB 113-F	GX32018	25°13.824'	70°14.452'	1550	3410 ± 90	3.7 (3.56–3.83)	<i>Abrocoma</i>	8
SDB 145-A	GX32020	25°13.644'	70°15.099'	1650	14,190 ± 470	17.3 (16.84–17.89)	<i>Abrocoma</i>	8
SDB 113-A	CAMS-133246	25°13.819'	70°14.447'	1550	23,000 ± 130	27.9 (27.68–28.06)	<i>Phyllotis</i>	6
SDB 113-B	GX32019	25°13.820'	70°14.448'	1550	23,280 ± 1230	27.9 (26.35–29.41)	<i>Phyllotis</i>	5
CTT 71	CAMS-133248	24°20.152'	70°07.952'	1900	17,800 ± 70	21.3 (21.18–21.45)	<i>Abrocoma</i>	5
CTT 72	CAMS-133249	24°20.152'	70°07.952'	1900	23,290 ± 130	28.1 (27.94–28.33)	<i>Abrocoma</i>	5
BZT 157	AA69850	24°05.384'	70°10.334'	1177	16,160 ± 120	19.3 (18.98–19.11)	<i>Abrocoma/Phyllotis</i>	3
<i>Quebrada Juncal</i>								
QJU 688	UGAMS-3141	25°44.337'	69°23.717'	2758	100 ± 20	0.1 (0.03–0.25) (Modern)	<i>Abrocoma</i>	9
QJU 689-B	UGAMS-3142	25°44.337'	69°23.717'	2758	370 ± 20	0.5 (0.33–0.49)	<i>Abrocoma</i>	7
QJU 690*	UGAMS-3144	25°44.377'	69°23.967'	2742	820 ± 20	0.7 (0.70–0.74)	<i>Abrocoma</i>	4
QJU 691	UGAMS-3145	25°44.377'	69°23.967'	2742	860 ± 20	0.8 (0.74–0.78)	<i>Abrocoma</i>	4
QJU 678-B	UGAMS-3143	25°44.319'	69°23.862'	2769	2230 ± 20	2.2 (2.16–2.32)	<i>Abrocoma</i>	7
QJU 678-C	AA65822	25°44.420'	69°22.808'	2822	5341 ± 63	6.1 (6.00–6.21)	<i>Abrocoma</i>	7
QJU 687	AA65820	25°44.668'	69°23.858'	2765	15,740 ± 130	18.9 (18.70–19.23)	<i>Phyllotis</i>	17
QJU 689-A	AA65821	25°44.668'	69°23.858'	2765	29,900 ± 440	34.5 (34.03–34.98)	<i>Phyllotis</i>	13

*Midden analysed only for macrofossils.

†Median probability and in parentheses minimum and maximum ages based on 1 SD intercepts.

using arithmetic averages) cluster analysis using the Multi-Variate Statistical Package for Windows to establish comparisons between pollen and macrofossil assemblages for each midden at any given locality and to identify specific plant macrofossil and pollen zones (Grimm, 1987). UPGMA uses the binomial Jaccard coefficient for macrofossil samples and Euclidean distances for pollen.

Modern analogue

We developed a modern analogue (necessary to control for the presence of extralocal species) using two different approaches. First, we collected all plant species present to within 500 m around each midden site. The local plant specimens were incorporated into our laboratory reference

collection mentioned above. Second, we collected and identified plant remains from two modern middens: one at QJU (0.1 ka) and another at SDB (not dated, but identified as modern by the presence of chlorophyll and pigmentation in preserved leaves). The modern middens were also used to establish present-day pollen assemblages at these localities.

Plant species found in our middens were classified by phytogeographical affinity (Table 3) [i.e. Lomas, Micro-oases (in the hyperarid core), Prepuna, Puna, Steppe, Wetland (represented by the presence of Cyperaceae) or Desert widespread]. Phytogeographical affinities were established using three criteria: flora found currently (and collected) at or around the midden sites, previous vegetation surveys near the study sites, and from the literature (Arroyo *et al.*, 1998; Marticorena *et al.*, 1998; Squeo *et al.*, 1998; Luebert & Gajardo, 2000; Saiz *et al.*, 2000; Latorre, 2002; Latorre *et al.*, 2002). When a taxon occurred in three or more phytogeographical zones it was assigned to the 'Desert widespread' category. Species were classified as either local or extralocal by comparing the current presence/absence at a specific midden site and by comparison of the fossil plant assemblage with those present in modern middens.

RESULTS

Radiocarbon chronology

Twenty radiocarbon dates span the interval between 29,900 and 100 ¹⁴C years (34.5–0.1 ka), with uneven temporal coverage (Table 2). Faecal pellet size and morphology indicate that the middens were either made by the chinchilla rat (*Abrocoma*) or by leaf-eared mice (*Phyllotis* spp.) (Table 2). Although distinct plant taxa are readily distinguished in midden macrofossils, identification to genus or species is often difficult and relies on possessing the necessary reference material (especially seeds and fruits) (Fig. 4). The identified taxa and the total number of taxa found in each rodent midden were graphed separately (Figs 5 & 6). A total of 26 different taxa were identified (Table 3), with individual midden richness ranging from 2 to 17 taxa.

Coastal range middens

At present, plants are practically non-existent within the hyperarid core of the Atacama (1200–2600 m), but plants do occur rarely in some gullies and rock outcrops (micro-oases).

Table 3 Plant macrofossils identified in this study, nomenclature, life-form and phytogeographical affinity*,†.

Taxon	Family	Life form	Phytogeographic affinity	Plant part identified
Gymnospermae				
<i>Ephedra</i> cf. <i>rupestris</i>	Ephedraceae	Shrub	Micro-oases	Seeds, bark
Angiospermae				
cf. <i>Senecio</i>	Asteraceae	Shrub and subshrub	Desert widespread	Achenes
<i>Polyachyrus</i> sp.	Asteraceae	Subshrub	Lomas and micro-oases	Seeds
<i>Argylia</i> sp.	Bignoniaceae	Perennial herb	Desert widespread	Fruits
<i>Cryptantha diffusa</i>	Boraginaceae	Annual herb	Prepuna	Nutlets
<i>Cryptantha phaceloides</i>	Boraginaceae	Annual herb	Prepuna	Nutlets
<i>Cryptantha</i> spp.	Boraginaceae	Annual herb	Desert widespread	Leaves
Brassicaceae				
cf. <i>Mathewsia</i>	Brassicaceae	Perennial herb and subshrub	Desert widespread	Siliques
<i>Opuntia camachoi</i>	Cactaceae	Perennial herb	Puna and prepuna	Seeds
<i>Atriplex</i> cf. <i>imbricata</i>	Chenopodiaceae	Shrub and subshrub	Micro-oases	Fruits, leaves
<i>Chenopodium</i> sp.	Chenopodiaceae	Perennial and annual herb	Lomas and micro-oases	Seeds
cf. <i>Scirpus</i>	Cyperaceae	Perennial herb	Wetlands	Seeds
<i>Adesmia atacamensis</i>	Fabaceae	Shrub	Prepuna and micro-oases	Leaves
<i>Adesmia</i> sp.	Fabaceae	Perennial and annual herb	Desert widespread	Seeds
<i>Phacelia cumingii</i>	Hydrophyllaceae	Annual herb	Puna and prepuna	Seeds
<i>Phacelia pinnatifida</i>	Hydrophyllaceae	Perennial and annual herb	Prepuna	Seeds
<i>Malesherbia</i> sp.	Malesherbiaceae	Perennial and annual herb	Lomas and micro-oases	Seeds
<i>Dinemandra ericoides</i>	Malphigaceae	Shrub	Lomas and micro-oases	Seeds
<i>Cristaria</i> spp.	Malvaceae	Perennial and annual herb	Desert widespread	Seeds
<i>Nolana</i> spp.	Solanaceae	Perennial and annual herb	Lomas and micro-oases	Nutlets
<i>Stipa frigida</i>	Poaceae	Perennial herb	Steppe	Florets
<i>Cistanthe</i> spp.	Portulacaceae	CAM annual herb	Desert widespread	Seeds, leaves
<i>Lycium</i> sp.	Solanaceae	Shrub	Prepuna and lomas	Fruits, seeds
<i>Junellia</i> sp.	Verbenaceae	Shrub	Puna and prepuna	Seeds

*Based on data from Arroyo *et al.* (1998), Marticorena *et al.* (1998), Squeo *et al.* (1998), Luebert & Gajardo (2000), Saiz *et al.* (2000), Latorre (2002) and Latorre *et al.* (2002).

†Prepuna, puna and steppe occur in the Andes.

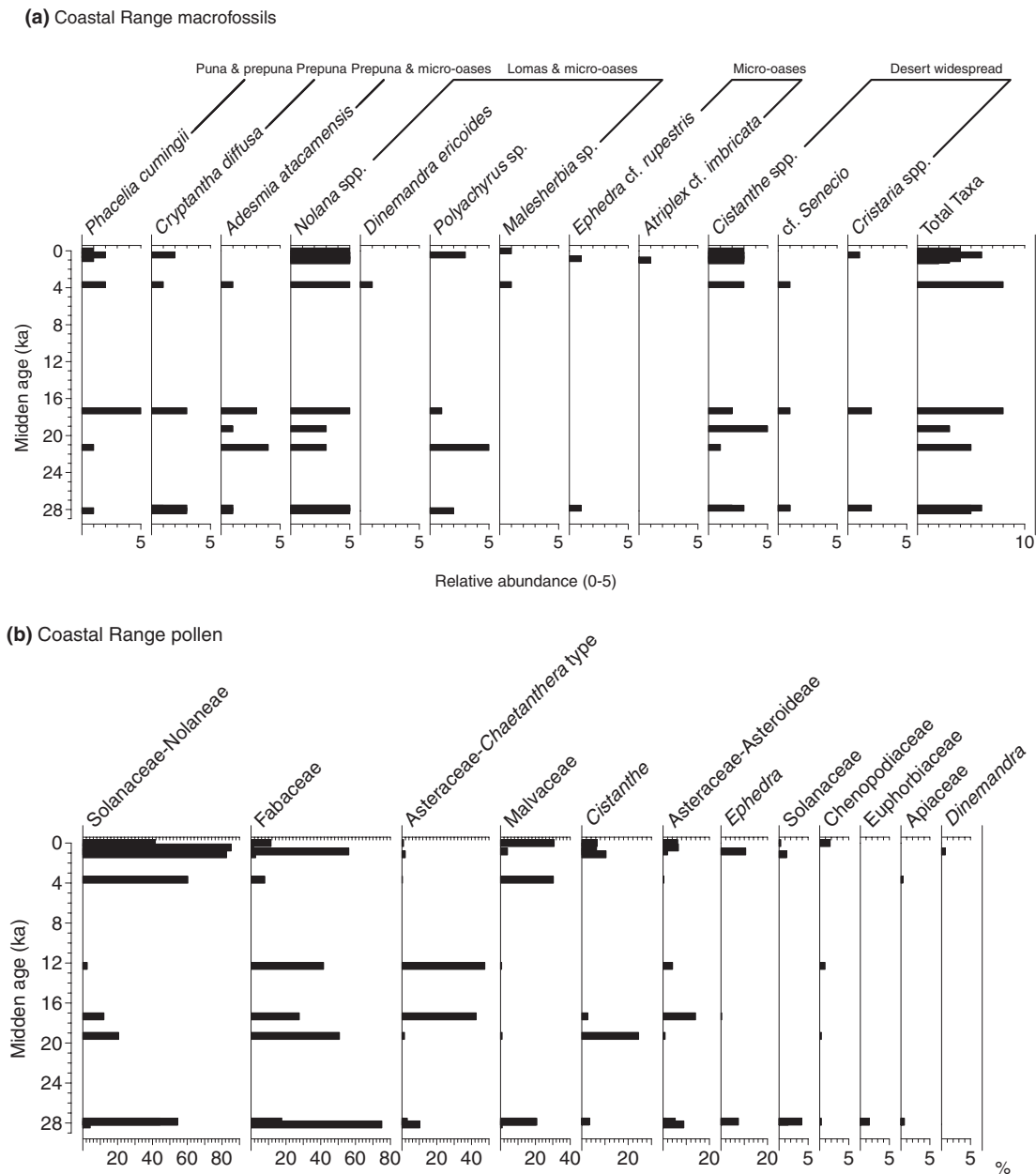


Figure 5 Coastal Range series. (a) Plant macrofossil diagram (13 middens). The total number of taxa present in each midden is shown in 'Total Taxa'. Relative abundance was estimated by using a relative abundance index (where 0 is absent and 5, dominant). (b) Midden matrix pollen diagram (11 middens). The total pollen sum for each sample included a minimum of 300 grain counts.

We identified eight taxa from our fossil middens: *Nolana* sp., *Cistanthe* sp., *Huidobria fruticosa*, *Dinemandra ericoides*, *Cristaria* sp., *Polyachyrus* sp., *Phacelia cumingii* and an unidentified Solanaceae (probably *Reyesia*) (Fig. 4). Three of these species occur today at SDB (*Nolana leptophylla*, *Cistanthe* sp. and *Cristaria* sp.) and two at BZT (*Cistanthe* sp. and *Nolana* sp.). At a slightly higher elevation (c. 800 m), the modern floras at CTT are slightly more diverse with the addition of *Polyachyrus* sp., *Dinemandra ericoides*, *Huidobria fruticosa*, *Phacelia cumingii* and cf. *Reyesia* aside from those species previously mentioned.

As with the modern landscape, all of our Coastal Range middens were dominated by *Nolana* sp. and *Cistanthe* sp. (Fig. 5a). Middens dated to 19.3, 1.1, 1.0, 0.9, 0.5 ka and the modern sample all fall into this category. Middens dated to 27.9–28.1 ka and at 21.3 ka as well as those dated to 17.3, 3.7 and 0.5 ka, however, show significant increases in plant richness and/or the presence of extralocal species such as *Adesmia atacamensis* and *Cryptantha diffusa*.

Pollen analyses of our oldest samples (27.9–28.1 ka) are dominated by Solanaceae–Nolaneae, Fabaceae and Malvaceae;

similar to the modern spectra but more diverse and with higher percentages of Fabaceae (Fig. 5b). Between 21.3 and 17.3 ka, the vegetation is dominated by Fabaceae, Asteraceae–Asteroideae and Asteraceae–*Chaetanthera* type (including *Polyachyrus*), low proportions of Solanaceae–Nolaneae and

the absence of Malvaceae. From 3.7 ka onwards, Solanaceae–Nolaneae pollen again dominates the spectra, initially with Malvaceae but with lower richness than at present. Pollen assemblages are more diverse after 1.1 ka, although Solanaceae–Nolaneae remains dominant. These younger middens

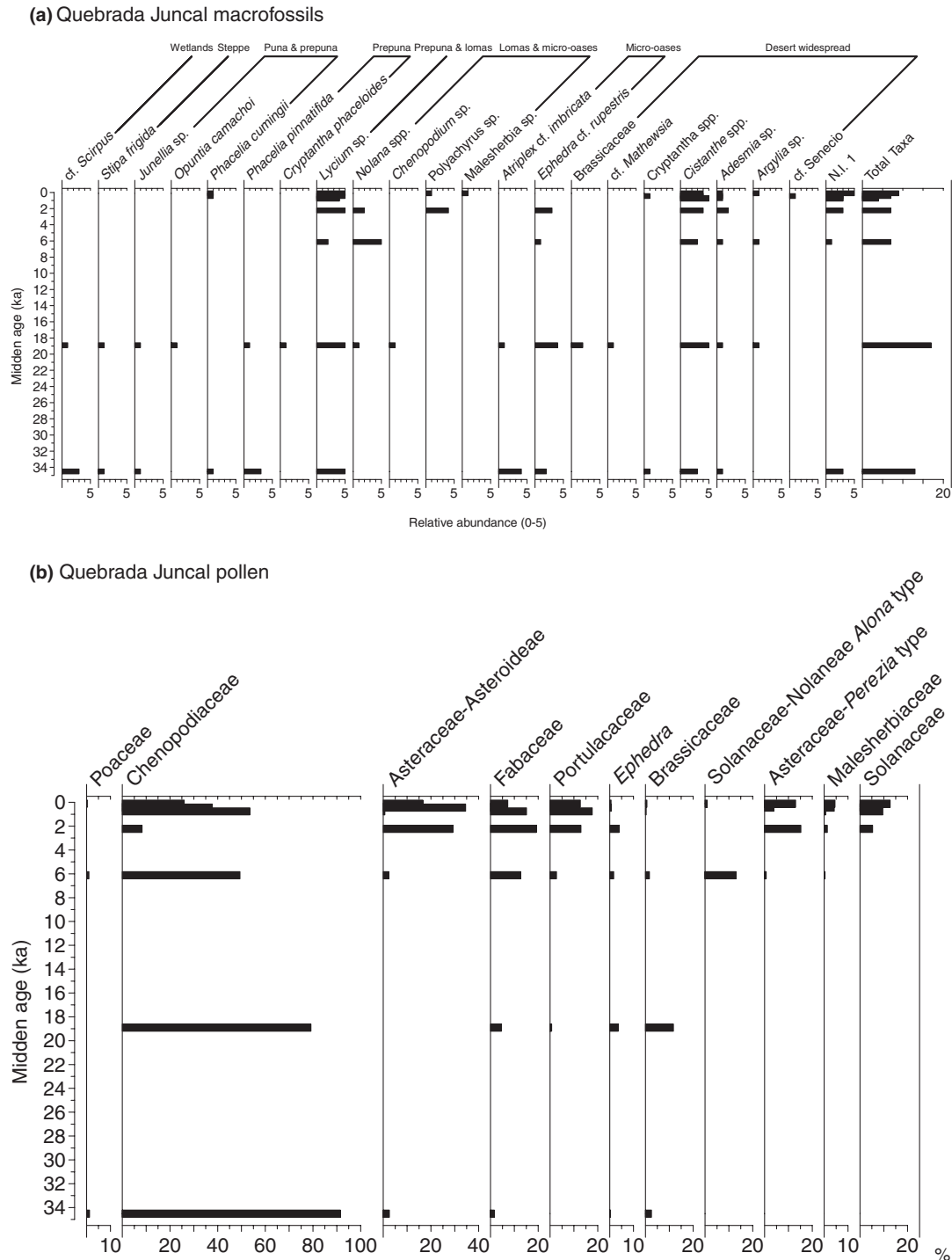


Figure 6 Quebrada Juncal series. (a) Plant macrofossil diagram (eight middens). The total number of taxa present in each midden (including one unknown taxon (N.I. 1)) is shown in 'Total Taxa'. Relative abundance was estimated by using a relative abundance index (where 0 is absent and 5, dominant). (b) Pollen diagram (seven middens) pollen sum for each sample included a minimum of 300 grains.

also have Fabaceae, Malvaceae, Asteraceae and *Cistanthe* pollen, among others.

Quebrada Juncal (Precordillera middens)

The Quebrada Juncal drainage currently reaches into the high-elevation Cordillera de Domeyko (with peaks over 5000 m) and is closely linked with the Andean Prepuna and Puna. We collected eight plant taxa in this area today, most within the confines of the valley bottom (*Senecio* spp., *Nolana* spp., *Atriplex imbricata*, *Phacelia cumingii*, *Adesmia atacamensis*, *Cistanthe* sp.). The arid slopes (where the middens were collected) are much less diverse, with *Cistanthe* and *Nolana* among the most common genera.

A prominent increase in macrofossil richness (Fig. 6a) along with the appearance of extralocals *Phacelia pinnatifida*, *Stipa frigida* and *Junellia* sp. occurs in middens dated at 34.5 and 18.9 ka. Cyperaceae seeds also occur in these middens (there are no active wetlands today in the valley). All the younger middens dated between 6.1 to 0.1 ka are similar in composition, with low taxonomic richness.

Pollen analyses (Fig. 6b) reveal two very different groups of middens. One group is made up of Pleistocene middens, which exhibit low richness and are dominated by Chenopodiaceae. The other group is made up of younger Holocene middens that evince higher diversity and the appearance of Asteraceae–Asteroideae, Portulacaceae, Solanaceae–Nolaneae and Malesherbiaceae, among others.

Cluster analyses

Cluster analysis based on Jaccard's similarity index for Coastal Range midden macrofossils generates two major clusters (Fig. 7a). The first cluster includes middens dated to 19.3, 1.1, 1.0, 0.9 and 0.5 ka and includes the modern midden. The second cluster contains mostly Pleistocene middens (28.1, 27.9, 21.3 and 17.3 ka) but also includes two much younger middens (3.7 and 0.5 ka).

Cluster analysis of pollen data from the Coastal Range (Fig. 7b) also reveals two large midden clusters and an additional midden (dated to 17.3 ka) that did not group with the previous clusters. As seen in Fig. 7(b), these clusters are slightly different in terms of the constituent middens than those generated for the macrofossils. The first cluster includes the 0.9 ka SDB midden along with all the Pleistocene middens from our northern sites (BZT and CTT). The second cluster includes the modern SDB midden together with a Pleistocene midden (27.9 ka) and a Holocene midden (3.7 ka). These analyses reveal that the 17.3 ka midden pollen is very different from all of our other coastal middens.

Large differences exist between the Holocene and the Pleistocene clusters [which includes both Last Glacial Maximum (LGM) and last glacial–interglacial transition middens] of macrofossils for the middens collected at Quebrada Juncal

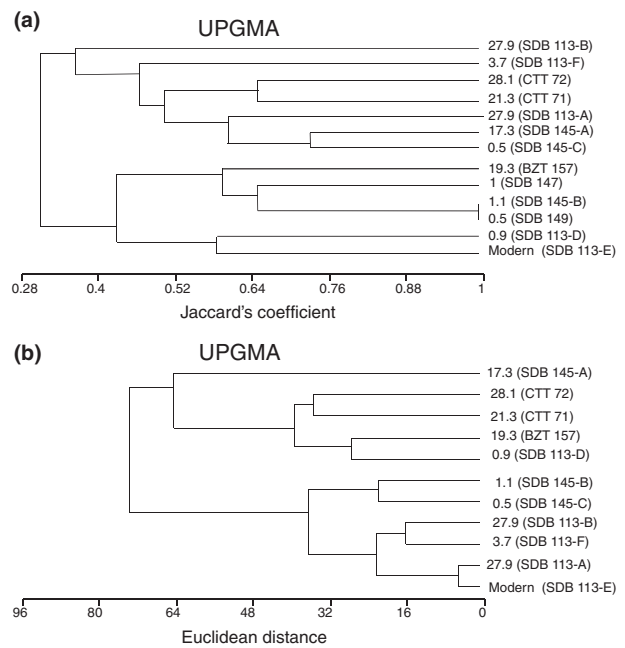


Figure 7 UPGMA cluster analyses indicating the similarity among midden (a) plant macrofossils and (b) pollen from the Coastal Range series (all ages in ka). BZT, Barzarte; SDB, Sierra del Buitre; CTT, Cerro Tres Tetras.

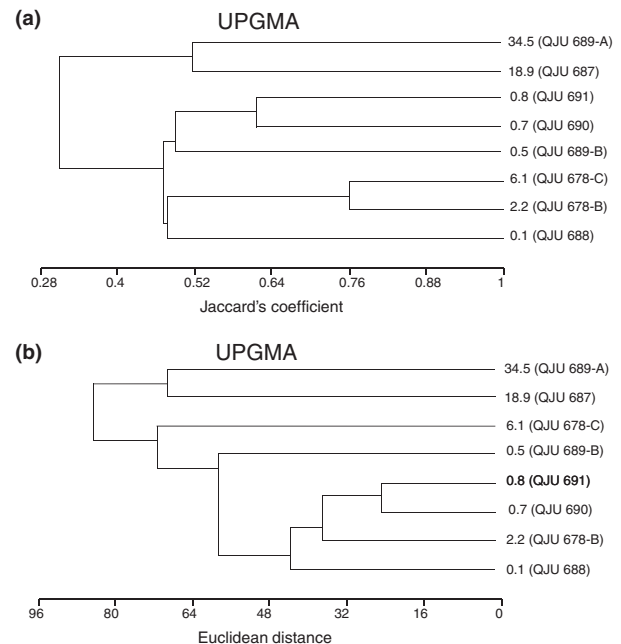


Figure 8 UPGMA cluster analyses indicating the similarity among midden (a) plant macrofossils and (b) pollen from the Quebrada Juncal (QJU) series (all ages in ka).

(Precordillera) (Fig. 8a). Pleistocene middens typically possess double the number of taxa (i.e. compare Fig. 4a and b) present in their Holocene counterparts (see also Table 2). These same clusters are also revealed by the similarity analyses on midden pollen (Fig. 8b).

DISCUSSION

A chronology of past ecological and hydrological change in the coastal Atacama

In northern Chile, modern ecological studies have shown that plant species richness increases in proportion with precipitation (Villagrán *et al.*, 1983; Arroyo *et al.*, 1988, 1998; Marquet *et al.*, 1998; Squeo *et al.*, 1998; Latorre, 2002). Midden taxonomic richness, however, is problematic because we cannot specify the duration of the depositional episode. Instead, the presence of extralocal taxa can be used as a surrogate for past precipitation increases. We can also track changing precipitation sources by examining the phytogeographical affinity of the extralocal species present in these middens (Table 3) (see also Latorre *et al.*, 2002, 2006). Modern taphonomic studies suggest that in the Atacama, midden-building rodents are generalists and therefore the surrounding local flora is well represented in our samples (Cortés *et al.*, 2002; Latorre *et al.*, 2003).

Plant macrofossil abundance in middens may not be representative of the plant cover on the adjacent landscape (Spaulding *et al.*, 1990). We thus emphasize changes in the dominant taxa and macrofossil presence/absence or richness rather than shifting patterns in plant macrofossil abundance (Betancourt *et al.*, 1990). Midden pollen is clearly more mobile than macrofossils and can reach a midden in many ways, not just via a rodent vector. Hence, midden pollen could potentially be suitable for estimating local plant abundance. A recent study revealed a good correspondence between pollen preserved in a midden matrix and local pollen rain and vegetation assemblages from northern Chile (de Porras *et al.*, 2010). Despite the often complex taphonomy that can affect pollen deposition in rodent middens (Maldonado *et al.*, 2005) the little work that has been accomplished is promising, and it is thus interesting to compare midden pollen with macrofossil records and the different spatial scales they represent.

Among our most surprising results is the presence of Andean extralocals in our Coastal Range middens from the last glacial period and last glacial–interglacial transition. Excepting a 19.3 ka midden from BZT, the majority of these middens display elevated macrofossil richness (Fig. 5) and diverse pollen assemblages. We cannot resolve changes between the last glacial period and the last glacial–interglacial transition due to a lack of a sequential midden series from any single locality except Sierra del Buitre. Even there, the midden series has a large temporal gap (including the LGM) between 27.9 and 17.3 ka.

Cluster analyses reveal two midden groups in the Coastal Range (Fig. 7): a group of last glacial–interglacial transition and glacial middens with elevated richness (compared with the present day) and a group of Holocene ‘modern’ middens. With just three taxa (two of them found locally), the only exception to the late Pleistocene cluster is a 19.3 ka midden collected at BZT (Table 2). This locality is *c.* 130 km further north than the SDB sites and is part of a different watershed (Fig. 1) so

direct comparisons are unwarranted (the SDB sites are today slightly more diverse). Nevertheless, the BZT midden is comparable with both CTT middens (28.1 and 21.3 ka) from the same watershed but at a slightly different elevation (the CTT sites are *c.* 800 m higher) (Fig. 1). The lower macrofossil richness of the BZT midden would thus imply that available moisture was considerably lower at 19.3 ka than at 28.1 or 21.3 ka. Notwithstanding the former, pollen analyses indicate that the BZT and CTT middens are practically indistinguishable and both are included in the same cluster (Fig. 7b). Thus the differences seen in the macrofossils may be due more to aspects of the local vegetation present at each of these ‘micro-oases’ than truly large differences in past climate change.

Elevated midden macrofossil richness, wetland taxa and numerous extralocals, such as *Phacelia pinnatifida* and the steppe grass *Stipa frigida*, can be attributed to past increases in local rainfall at 34.5 and 18.9 ka at Quebrada Juncal (QJU) in the Andean Precordillera (Fig. 6a). The QJU macrofossils and pollen assemblages separate into clearly differentiated groups (Fig. 8). The equivalent pollen assemblages at 34.5 and 18.9 ka are swamped by Chenopodiaceae pollen (probably *Atriplex*, a very productive pollen producer), which could have resulted either from an active wetland within the confined valley or elevated local abundance of *Atriplex cf. imbricata* present on the slopes during the Pleistocene (not present on these slopes today but abundant in the 34.5 and 18.9 ka middens). As percentages of Chenopodiaceae drop in our Holocene middens, the pollen assemblages become much more diverse (Fig. 6b). This perhaps resulted from an increase in the representation of the hillslope flora as the wetland diminished in importance and/or completely disappeared within the Holocene pollen assemblages.

In any case, most of the extralocal species present at our sites within QJU during the late Pleistocene probably migrated either southwards or downslope from their current elevations in the Puna and Prepuna as a consequence of increased local rainfall. Coeval pluvial events have also been documented just 30 km further north at Quebrada del Chaco at even lower elevations (*c.* 2600 m) (Maldonado *et al.*, 2005). In contrast, middens with the same number or fewer species than those of our modern samples probably reflect overall drier conditions. All the Holocene middens collected at QJU fall into this category, as do the majority of the youngest middens from Sierra del Buitre.

A widespread major summer pluvial event occurred between *c.* 17.5 and 9.0 ka along the western slope of the Andes (i.e. the Central Andean Pluvial Event or CAPE) and is thoroughly documented in a diverse array of palaeoclimatic records (Betancourt *et al.*, 2000; Grosjean *et al.*, 2001; Latorre *et al.*, 2002, 2003, 2006; Rech *et al.*, 2002; Placzek *et al.*, 2006, 2009; Nester *et al.*, 2007; Quade *et al.*, 2008). CAPE was spatially extensive, even affecting areas such as Quebrada del Chaco (Maldonado *et al.*, 2005) and perhaps reaching as far south as 31° S in the Doña Rosa mountains (Zech *et al.*, 2007). The Coastal Range was also affected by increased groundwater discharge during the CAPE, as recent evidence from Quebrada

Agua de Cascabel (the canyon that drains the SDB) indicates an episode of major wetland expansion at *c.* 13.7 ka (C.L., unpublished data).

South of 25° S, a pluvial event of extratropical origin occurred earlier than the CAPE between *c.* 43 and 37 ka and during the LGM, *c.* 24–18 ka in the Andean Precordillera (Maldonado *et al.*, 2005). Aside from the evidence presented here for the Coastal Range at CTT, there is no previous evidence for a LGM pluvial event north of 25° S in the Atacama (Latorre *et al.*, 2005). This lends support to our hypothesis that increased runoff and groundwater discharge are probably just as important in explaining the presence of extralocal taxa in our records as increases in local rainfall.

The Holocene vegetation in the coastal Atacama was for the most part similar to the present, although important hydrological changes did occur, as documented both here and in other records. An increase in available moisture at 3.7 ka at SDB is a good example. Similar wet periods are also recorded in Río Salado (3.5–2.3 ka) (Latorre *et al.*, 2006) and Pampa Vizcachilla (3.4–3.3 ka) middens (Latorre *et al.*, 2003) and in a salt core from Salar de Atacama (6.2–3.5 ka) (Bobst *et al.*, 2001). Hence, the most likely explanation for the diverse plant assemblages present at SDB at 3.7 ka is that increased rainfall at upper elevations facilitated the colonization of lower-elevation valleys and canyons through increased runoff and episodic floods. Nevertheless, our chronologies reveal that this might not be the only source of moisture during the Holocene. For example, a very diverse assemblage occurs in SDB at 0.5 ka. Yet a midden of equivalent age at QJU has very low taxonomic richness. This could imply the presence of local rainfall events restricted to the Coastal Range, perhaps related to increased number of polar outbreaks (e.g. Vuille & Ammann, 1997).

Implications for the biogeography of the coastal Lomas

None of our Coastal Range middens contain plant species that are exclusive of the Lomas (such as *Gypothamnium pinifolium* or *Oxyphyllum ulicinum*) (Table 3). This implies that the obligate coastal fog oasis species remained at the same or at lower elevations than today during the full glacial and the last glacial–interglacial transition. Sea level was 100–150 m lower and weakening of the South Pacific subtropical anticyclone (Kitoh & Murakami, 2002; Rojas *et al.*, 2009) would have disrupted the temperature inversion along the Chilean coast, most likely weakening advective fog intensity and extent. Instead, moisture along the Coastal Range must have originated from sources other than fog to explain past increases in richness in our middens. As previously stated, this probably resulted from either increased winter rainfall or summer rainfall that drained superficially along major east–west trending canyons and valleys originating in the Andes and by increased groundwater discharge. The appearance of the Andean species *Cryptantha diffusa*, *Phacelia cumingii* and *Adesmia atacamensis* suggest an Andean source of moisture for a brief pre-LGM interval from 28.1 to 27.9 ka that has not been

previously documented in the Atacama. Nevertheless, several taxa present in our middens do occur in the ‘Lomas and micro-oases’ (such as *Dinemandra ericoides* and *Polyachyrus*). The presence of these taxa during the last glacial–interglacial transition at our sites in the coastal cordillera indicates that they might have opportunistically migrated upslope from the Lomas or from other micro-oases during these periods of increased runoff/discharge.

Overall, our results suggest that increases in winter and summer rainfall have been important regarding hydrological change in the present absolute desert. Increased summer rainfall and concomitant elevational descent led to many Puna and Steppe taxa invading the Prepuna between 17.5 and 9.5 ka north of 25° S (see review in Latorre *et al.*, 2007). To the south, the descent of Andean species most likely reduced the areal extent of the absolute desert during the late Quaternary (Maldonado *et al.*, 2005). Hence, this formidable barrier to dispersal was crossed by plant species from higher elevations and even Andean taxa appear in the hyperarid Coastal Range during the LGM and the last glacial–interglacial transition. Species from both Andean and Lomas floras very likely interacted to some extent during these widespread pluvials.

These species interactions during the last glacial–interglacial transition and other Pleistocene pluvial events could result in the current Andean–coastal disjunctions of genera such as *Mathewsia* and *Lycium*, and of species such as *Adesmia atacamensis*, which today is widespread throughout the Prepuna but is also present in the upper Coastal Range and in micro-oases immersed within the absolute desert. More palaeoecological records, coupled with phylogeographies of these desert plants, will be needed to fully disclose these biogeographical insights.

Today, nearly continuous vegetation corridors between the Andes and the lowlands only exist south of *c.* 27° S. This southern limit of the absolute desert might have shifted *c.* 1° (*c.* 110 km) to the north multiple times during the glacial period and last glacial–interglacial transition (Maldonado *et al.*, 2005), but apparently not any further. The extent of this shift is constrained by intensive sampling of carbon and oxygen isotopes from soil carbonate along three elevation transects from the coast to the High Andes between 22.5 and 25° S (Quade *et al.*, 2007). The isotopic evidence suggests that vegetation was displaced *c.* 500 m downslope into absolute desert at its upper limits. The lack of soil carbonate formation at the driest elevations (2300–1000 m), and carbon isotope values from trace quantities of carbonate that are in equilibrium with the atmosphere (+2 to +4‰) suggest that the hyperarid and plantless core of the central Atacama Desert persisted through the Quaternary and possibly the late Neogene. Apparently, pedogenic carbonate does not form in the absence of vegetation because root respiration and bicarbonate production, along with other factors, are essential for its genesis (Quade *et al.*, 2007).

The persistence of absolute desert throughout the Quaternary means that long-distance dispersal events of *c.* 100 km are still necessary to account for the establishment of Andean

plants in either the *Lomas* or the lower fringes of what is now absolute desert. Evidence for long-distance dispersal and the high mobility of Atacama flora is available from the northern Atacama, where between February and March, AD 1600 the Huaynaputina eruption denuded a large area between 1600 and 2600 m near Moquegua c. 120 km from the coast in southern Peru (Schwarzer *et al.*, 2010). Disjunct, isolated plant populations of the *Lomas*-like flora on the pumice slopes, dominated by ephemerals and annuals, provide evidence for long-distance dispersal, with likely source populations one to several hundred kilometres away. Our midden data support Schwarzer *et al.*'s (2010) conclusion that dispersal limitations imposed by the absolute desert are probably secondary in importance to the frequency of climatic conditions favourable for plant establishment.

Long-distance dispersal events between the Andes and the lower fringes of absolute desert or the *Lomas* could have happened in any number of ways. For example, the Andean fox (*Lycolopex culpaeus*) consumes fruits to supplement its diet and is known to roam large distances in the Atacama and northern Chile. Although it may be an ineffective and inefficient disperser (Bustamante *et al.*, 1992; Castro *et al.*, 1994; Leon-Lobos & Kalin-Arroyo, 1994; Silva *et al.*, 2005), the Andean fox is still a legitimate source of long-distance dispersal, as are granivorous birds in both the Andes and the *Lomas*. Another less acknowledged source of dispersal is the rare but extreme floods that originate in the High Andes and cross the Central Depression to the lower fringes of the absolute desert and the coast. Such extreme floods may have been more extensive and frequent in the past (Lamy *et al.*, 2000), and could have transported both water and propagules from the Andes to suitable establishment sites in the lower fringes of the absolute desert. Extreme flood events probably happened during pluvial events, when regional groundwater levels were elevated in the Central Depression and supported local wetlands harbouring Andean plants. This would have shortened dispersal distances by floods, birds and mammals.

CONCLUSIONS

Our unique record reveals important past vegetation changes even in the hyperarid core of the central–southern Atacama. These changes were the result of major hydrological change during specific events during the late Quaternary, for the most part tied to the last glacial–interglacial transition and the late Holocene. At present this zone is almost completely devoid of any vegetation and rainfall is $< 1 \text{ mm year}^{-1}$ (Houston, 2006b). Yet our results show periods of elevated plant species richness and the presence of Andean extralocal species in the Coastal Ranges during the late Pleistocene at 28.1–27.9, 21.3 and 17.3 ka and for the late Holocene at 3.7 and 0.5 ka. Similar events occurred at 34.5 and 18.9 ka in the neighbouring Precordillera at QJU.

A forbidding zone of absolute desert, at times slightly contracted, persisted throughout the Quaternary and possibly the Neogene, but did not limit episodic, long-distance

colonization events of plants from the Andes to the Coast. These colonization events happened during pluvial times when establishment conditions were favourable and dispersal distances by birds, mammals and floods might have been shortened by the existence of local wetlands in the Central Depression. This contradicts the idea that the coastal *Lomas* communities have remained isolated during the Quaternary and presents new prospects for understanding the evolution and diversity of the flora of the Atacama Desert.

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REFERENCES

- Alpers, C.N. & Brimhall, G.H. (1988) Middle Miocene climatic change in the Atacama Desert, northern Chile: evidence from supergene mineralization at La Escondida. *Geological Society of America Bulletin*, **100**, 1640–1656.
- Arroyo, M.T., Squeo, F.A., Armesto, J.J. & 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, M.T., Castor, C., Marticorena, C., Muñoz, M., Caviere, L., Matthei, O., Squeo, F., Grosjean, M. & Rodríguez, R. (1998) The flora of Lluillailaco National Park located in the transitional winter–summer rainfall area of the northern Chilean Andes. *Gayana Botánica*, **55**, 93–110.
- Baker, P.A., Seltzer, G.O., Fritz, S.C. *et al.* (2001) The history of South American tropical precipitation for the past 25,000 years. *Science*, **291**, 640–643.
- Betancourt, J., Van Devender, T. & Martin, P. (1990) *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson, AZ.
- Betancourt, J.L. & Saavedra, B. (2002) Paleomadrigueras de roedores, un nuevo método para el estudio del Cuaternario en zonas áridas de Sudamérica. *Revista Chilena de Historia Natural*, **75**, 527–546.
- Betancourt, J.L., Latorre, C., Rech, J.A., Quade, J. & Rylander, K.A. (2000) A 22,000-year record of monsoonal precipitation from northern Chile's Atacama Desert. *Science*, **289**, 1542–1546.
- Bobst, A.L., Lowenstein, T.K., Jordan, T.E., Godfrey, L.V., Hein, M.C., Ku, T.-L. & Luo, S. (2001) A 106 ka paleocli-

- mate record from drill core of the Salar de Atacama, northern Chile. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **173**, 21–42.
- Bustamante, R.O., Simonetti, J.A. & Mella, J.E. (1992) Are foxes legitimate and efficient seed dispersers? A field test. *Acta Oecologia*, **13**, 203–208.
- Castro, S.A., Silva, S.I., Meserve, P.L., Gutierrez, J.R., Contreras, L.C. & Jaksic, F.M. (1994) Frugivoría y dispersión de semillas de pimienta (*Schinus molle*) por el zorro culpeo (*Pseudalopex culpaeus*) en el Parque Nacional Fray Jorge (IV Región, Chile). *Revista Chilena de Historia Natural*, **67**, 169–176.
- Cereceda, P., Larrain, H., Osses, P., Fariás, M. & Egaña, I. (2008) The spatial and temporal variability of fog and its relation to fog oases in the Atacama Desert, Chile. *Atmospheric Research*, **87**, 312–323.
- Clement, A., Hall, A. & Broccoli, A.J. (2004) The importance of precessional signals in the tropical climate. *Climate Dynamics*, **22**, 327–341.
- Cortés, A., Miranda, E. & Jiménez, J.E. (2002) Seasonal food habits of the endangered long-tailed chinchilla (*Chinchilla lanigera*): the effect of precipitation. *Mammalian Biology*, **67**, 167–175.
- Diaz, H.F. & Bradley, R.S. (2004) The Hadley circulation: present, past and future. An introduction. *The Hadley circulation: present, past and future* (ed. by H.F. Diaz and R.S. Bradley), pp. 1–5. Kluwer Academic Publishers, Dordrecht.
- Dillon, M.O. (2005) The Solanaceae of the Lomas formations of Coastal Peru and Chile. *The legacy of a taxonomist* (ed. by V. Hollowell, T. Keating, W. Lewis and T. Croat). *Monographs in Systematic Botany from the Missouri Botanical Garden*, **104**, 131–155.
- Dillon, M.O., Tu, T., Xie, L., Quipuscoa Silvestre, V. & Wen, J. (2009) Biogeographic diversification in *Nolana* (Solanaceae), a ubiquitous member of the Atacama and Peruvian Deserts along the western coast of South America. *Journal of Systematics and Evolution*, **47**, 457–476.
- Dunai, T.J., López, G.A.G. & Juez-Larré, J. (2005) Oligocene–Miocene age of aridity in the Atacama Desert revealed by exposure dating of erosion-sensitive landforms. *Geology*, **33**, 321–324.
- Faegri, K. & Iversen, J. (1989) *Textbook of pollen analysis*, 4th edn. Blackwell Science Ltd, 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.
- Garreaud, R., Barichivich, J., Christie, D.A. & Maldonado, A. (2008) Interannual variability of the coastal fog at Fray Jorge relict forests in semiarid Chile. *Journal of Geophysical Research*, **113**, 1–16.
- Gengler-Nowak, K. (2002) Reconstruction of the biogeographical history of Malesherbiaceae. *The Botanical Review*, **68**, 171–188.
- Grimm, E. (1987) CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, **13**, 13–35.
- 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. *Journal of Paleolimnology*, **14/3**, 241–252.
- Grosjean, M., van Leeuwen, J.F.N., van der Knaap, W.O., Geyh, M.A., Ammann, B., Tanner, W., Messerli, B., Valero-Garcés, B. & Veit, H. (2001) A 22000 ¹⁴C yr B.P. sediment and pollen record of climate change from Laguna Miscanti (23° S), northern Chile. *Global and Planetary Change*, **28**, 35–51.
- Heusser, C.J. (1983) Quaternary palynology of Chile. *Quaternary of South America and Antarctic Peninsula*, **1**, 5–22.
- Hillyer, R., Valencia, B.G., Bush, M.B., Silman, M.R. & Steinitz-Kannan, M. (2009) A 24,700-yr paleolimnological history from the Peruvian Andes. *Quaternary Research*, **71**, 71–82.
- Houston, J. (2006a) The great Atacama flood of 2001 and implications for Andean hydrology. *Hydrological Processes*, **20**, 591–610.
- Houston, J. (2006b) Variability of precipitation in the Atacama Desert: its causes and hydrological impact. *International Journal of Climatology*, **26**, 2181–2198.
- Johnston, I.M. (1929) Papers on the flora of northern Chile. *Contributions to the Gray Herbarium*, **85**, 1–172.
- Kim, J., Schneider, R.R., Hebbeln, D., Müller, P.J. & Wefer, G. (2002) Last deglacial sea-surface temperature evolution in the Southeast Pacific compared to climate changes on the South American continent. *Quaternary Science Reviews*, **21**, 2085–2097.
- Kitoh, A. & Murakami, S. (2002) Tropical Pacific climate at the mid-Holocene and the Last Glacial Maximum simulated by a coupled ocean–atmosphere general circulation model. *Paleoceanography*, **17**, 1047.
- Lamy, F., Klump, J., Hebbeln, D. & Wefer, G. (2000) Late Quaternary rapid climate change in northern Chile. *Terra Nova*, **12**, 8–13.
- Latorre, C. (2002) *Clima y vegetación del Desierto de Atacama durante el Cuaternario tardío, II Región, Chile*. PhD Thesis, Departamento de Ciencias Ecológicas, Universidad de Chile.
- 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 (lat 22°–24°S). *Geological Society of America Bulletin*, **114**, 349–366.
- Latorre, C., Betancourt, J.L., Rylander, K.A., Quade, J. & Matthei, O. (2003) A vegetation history from the arid prepuna of northern Chile (22–23°S) over the last 13 500 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194**, 223–246.
- Latorre, C., Betancourt, J.L., Rech, J.A., Quade, J., Holmgren, C., Placzek, C., Maldonado, A., Vuille, M. & Rylander, K.A. (2005) Late Quaternary history of the Atacama Desert. 23° S: the archaeology and environmental history of the southern deserts (ed. by M. Smith and P. Hesse), pp. 73–90. National Museum of Australia Press, Canberra.

- Latorre, C., Betancourt, J.L. & Arroyo, M.T. (2006) Late Quaternary vegetation and climate history of a perennial river canyon in the Río Salado basin (22°S) of northern Chile. *Quaternary Research*, **65**, 450–466.
- Latorre, C., Moreno, P.I., Vargas, G., Maldonado, A., Villamartínez, R., Armesto, J.J., Villagrán, C., Pino, M., Nuñez, L.A. & Grosjean, M. (2007) Late Quaternary environments and paleoclimate. *The geology of Chile* (ed. by T. Moreno and W. Gibbons), pp. 309–328. The Geological Society, London.
- Leon-Lobos, P.M. & Kalin-Arroyo, M.T. (1994) Germinación de semillas de *Lithrea caustica* (Mol.) H. et A. (Anacardiaceae) dispersadas por *Pseudalopex* sp. (Canidae) en el bosque esclerófilo de Chile Central. *Revista Chilena de Historia Natural*, **67**, 59–64.
- Luebert, F. & Gajardo, R. (2000) Vegetación de los Andes áridos del norte de Chile. *Lazaroa*, **21**, 111–130.
- Luebert, F., Wen, J. & Dillon, M.O. (2009) Systematic placement and biogeographical relationships of the monotypic genera *Gypothamnium* and *Oxyphyllum* (Asteraceae: Mutisioideae) from the Atacama Desert. *Botanical Journal of the Linnean Society*, **159**, 32–51.
- Maldonado, A., Betancourt, J.L., Latorre, C. & Villagrán, C. (2005) Pollen analyses from a 50 000-yr rodent midden series in the southern Atacama Desert (25° 30' S). *Journal of Quaternary Science*, **20**, 493–507.
- Marchant, M., Cecioni, A., Figueroa, S., González, H., Giglio, S., Hebbeln, D., Kaiser, J., Lamy, F., Mohtadi, M., Pineda, V. & Romero, O. (2007) Marine geology, oceanography and climate. *The geology of Chile* (ed. by T. Moreno and W. Gibbons), pp. 309–328. The Geological Society, London.
- Marquet, P.A., Bozinovic, F., Bradshaw, G.A., Cornelius, C., Gonzalez, H., Gutierrez, J.R., Hajek, E.R., Lagos, J.A., López-Cortés, F., Nuñez, L., Rosello, E.F., Santoro, C., Samaniego, H., Standen, V.G., Torres-Mura, J.C. & Jaksic, F.M. (1998) Los ecosistemas del Desierto de Atacama y área Andina adyacente. *Revista Chilena de Historia Natural*, **71**, 593–617.
- Martcorena, C., Matthei, O., Rodríguez, R., Arroyo, M., Muñoz, M., Squeo, F. & Arancio, G. (1998) Catálogo de la flora vascular de la Segunda región (Región de Antofagasta), Chile. *Gayana Botánica*, **55**, 23–83.
- Mohtadi, M., Romero, O.E. & Hebbeln, D. (2004) Changing marine productivity off northern Chile during the past 19 000 years: a multivariable approach. *Journal of Quaternary Science*, **19**, 347–360.
- Muñoz-Schick, M., Pinto, R., Mesa, A. & Moreira-Muñoz, A. (2001) 'Oasis de neblina' en los cerros costeros del sur de Iquique, región de Tarapacá, Chile, durante el evento El Niño 1997–1998. *Revista Chilena de Historia Natural*, **74**, 389–405.
- Nester, P.L., Gayo, E., Latorre, C., Jordan, T.E. & Blanco, N. (2007) Perennial stream discharge in the hyperarid Atacama Desert of northern Chile during the latest Pleistocene. *Proceedings of the National Academy of Sciences USA*, **104**, 19724–19729.
- Placzek, C., Quade, J. & Patchett, P. (2006) Geochronology and stratigraphy of late Pleistocene lake cycles on the Southern Bolivian Altiplano: implications for causes of tropical climate change. *GSA Bulletin*, **118**, 515–532.
- Placzek, C., Quade, J., Betancourt, J.L., Patchett, P.J., Rech, J.A., Latorre, C., Matmon, A., Holmgren, C. & English, N.B. (2009) Climate in the dry Central Andes over geologic, millennial, and interannual timescales. *Annals of the Missouri Botanical Garden*, **96**, 386–397.
- de Porras, M.E., González, L.A. & Maldonado, A. (2010) An experimental approach to improve the fossil rodent midden pollen analysis in northern arid and semiarid areas of Chile. *Abstracts – 2nd International Symposium: 'Reconstructing Climate Variations in South America and the Antarctic Peninsula over the last 2000 years', Valdivia, Chile, October 27–30, 2010*. Abstract 168. Available at: <http://www.cecs.cl/pages2010/AbstractBookPAGES2010.pdf>.
- Quade, J., Rech, J., Latorre, C., Betancourt, J., Gleason, E. & Kalin-Arroyo, M. (2007) Soils at the hyperarid margin: the isotopic composition of soil carbonate from the Atacama Desert. *Geochimica et Cosmochimica Acta*, **71**, 3772–3795.
- Quade, J., Rech, J.A., Betancourt, J.L., Latorre, C., Quade, B., Rylander, K.A. & Fisher, T. (2008) Paleowetlands and regional climate change in the central Atacama Desert, northern Chile. *Quaternary Research*, **69**, 343–360.
- Rech, J.A., Quade, J. & Betancourt, J.L. (2002) Late Quaternary paleohydrology of the central Atacama Desert (lat 22–24°S), Chile. *Geological Society of America Bulletin*, **114**, 334–348.
- Rech, J.A., Currie, B.S., Michalski, G. & Cowan, A.M. (2006) Neogene climate change and uplift in the Atacama Desert, Chile. *Geology*, **34**, 761–764.
- Rech, J.A., Currie, B.S., Shullenberger, E.D., Dunagan, S.P., Jordan, T.E., Blanco, N., Tomlinson, A.J., Rowe, H.D. & Houston, J. (2010) Evidence for the development of the Andean rain shadow from a Neogene isotopic record in the Atacama Desert, Chile. *Earth and Planetary Science Letters*, **292**, 371–382.
- Reimer, P.J., Baillie, M.G.L., Bard, E. *et al.* (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon*, **51**, 1111–1150.
- Rojas, M., Moreno, P.I., Kageyama, M., Crucifix, M., Hewitt, C., Abe, A., Ohgaito, R., Brady, E. & Hope, P. (2009) The Southern Westerlies during the last glacial maximum in PMIP2 simulations. *Climate Dynamics*, **32**, 525–548.
- Rundel, P. & Mahu, M. (1976) Community structure and diversity in a coastal fog desert in northern Chile. *Flora*, **165**, 493–505.
- 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.
- Rundel, P.W., Dillon, M.O. & Palma, B. (1996) Flora and vegetation of Pan de Azúcar National Park in the Atacama Desert of northern Chile. *Gayana Botánica*, **53**, 295–315.

- Saiz, F., Yates, L., Nuñez, C., Daza, M., Varas, M.E. & Vivar, C. (2000) Biodiversidad del complejo de artrópodos asociados al follaje de la vegetación del norte de Chile, II región. *Revista Chilena de Historia Natural*, **73**, 671–692.
- Schmithüsen, J. (1956) Die raumliche Ordnung der chilenischen Vegetation. *Bonner Geographische Abhandlungen*, **17**, 1–86.
- Schwarzer, C., Cáceres Huamaní, F., Cano, A., La Torre, M.I. & Weigend, M. (2010) 400 years for long-distance dispersal and divergence in the northern Atacama desert – Insights from the Huaynaputina pumice slopes of Moquegua, Peru. *Journal of Arid Environments*, **74**, 1540–1551.
- Silva, S.I., Bozinovic, F. & Jaksic, F.M. (2005) Frugivory and seed dispersal by foxes in relation to mammalian prey abundance in a semiarid thornscrub. *Austral Ecology*, **30**, 739–746.
- Spaulding, W.G., Betancourt, J.L., Croft, L.K. & Cole, K.L. (1990) Packrat middens: their composition and methods of analysis. *Packrat middens: the last 40,000 years of biotic change* (ed. by J.L. Betancourt, T.R. Van Devender and P.S. Martin), pp. 59–84. University of Arizona Press, Tucson, AZ.
- Squeo, F.A., Cavieres, L.A., Arancio, G., Novoa, J.E., Matthei, O., Marticorena, C., Rodriguez, R., Arroyo, M.T. & Muñoz, M. (1998) Biodiversidad de la flora vascular en la Región de Antofagasta, Chile. *Revista Chilena de Historia Natural*, **71**, 571–591.
- Stuiver, M. & Reimer, P.J. (1993) Extended ¹⁴C database and revised CALIB radiocarbon calibration program. *Radiocarbon*, **35**, 215–230.
- Villagrán, C., Arroyo, M.T.K. & Marticorena, C. (1983) Efectos de la desertización en la distribución de la flora andina de Chile. *Revista Chilena de Historia Natural*, **56**, 137–157.
- 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.
- Vuille, M., Bradley, R.S. & Keimig, F. (2000) Interannual climate variability in the Central Andes and its relation to tropical Pacific and Atlantic forcing. *Journal of Geophysical Research–Atmospheres*, **105**, 12447–12460.
- Zech, R., Kull, C., Kubik, P.W. & Veit, H. (2007) Exposure dating of late glacial and pre-LGM moraines in the Cordon de Doña Rosa, northern/central Chile (similar to 31 degrees S). *Climate of the Past*, **3**, 1–14.

BIOSKETCH

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