



ORIGINAL
ARTICLE



Late Quaternary climate change, relict populations and present-day refugia in the northern Atacama Desert: a case study from Quebrada La Higuera (18° S)

María Isabel Mujica^{1,2}, Claudio Latorre^{2,3*}, Antonio Maldonado^{4,5}, Leticia González-Silvestre⁴, Raquel Pinto⁶, Ricardo de Pol-Holz⁷ and Calogero M. Santoro^{8,9}

¹Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile, ²Institute of Ecology & Biodiversity (IEB), Ñuñoa, Santiago, Chile, ³Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile, ⁴Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad de La Serena, La Serena, Chile, ⁵Departamento de Biología Marina, Universidad Católica del Norte, Coquimbo, Chile, ⁶Universidad Arturo Prat, Iquique, Chile, ⁷Departamento de Oceanografía, Universidad de Concepción, Concepción, Chile, ⁸Instituto de Alta Investigación, Universidad de Tarapacá, Arica, Chile, ⁹Centro de Investigaciones del Hombre en el Desierto (CIHDE), Arica, Chile

ABSTRACT

Aim In deserts, past climate change (and particularly past rainfall variability) plays a large role in explaining current plant species distributions. We ask which species were most and which were least affected by changes in rainfall during the late Quaternary in northernmost Chile.

Location Quebrada La Higuera (QLH; 18° S), a shallow canyon that cuts east–west through the western Andean precordillera of northern Chile, connecting the Altiplano with the hyperarid Atacama Desert.

Methods We collected and dated 22 rodent middens from elevations of 3100–3500 m in QLH. These were analysed for identifiable plant macrofossils and pollen. We also measured chinchilla rat (*Abrocoma cinerea*) faecal pellets in the youngest middens to explore how they relate to past ecological and climatic change.

Results The three oldest middens dated to more than 37 ka (thousand calibrated ¹⁴C years), four middens dated to 14.4–11.6 ka, and fifteen middens spanned the last 650 years. During all the intervals examined, extralocal species (those found today at higher elevations and indicative of positive rainfall anomalies) were present at our midden sites. In the youngest interval, *Parastrephia* pollen (indicating increased rainfall) increased abruptly at AD 1760 and remained high until the mid-1800s. This increase was also seen in our faecal pellet record.

Main conclusions Extralocal species were prevalent in late Pleistocene middens at lower elevations when the climate was wetter. When combined with other regional midden records, we postulate that many species found today in the Altiplano were displaced to lower elevations during the late Pleistocene. The recent large-scale mortality documented among arboreal cactus populations along the present upper margins of the Atacama suggests that these are relict populations that are likely to have flourished during a wetter period in the early 1800s.

Keywords

Altiplano, Atacama Desert, central Andes, late Quaternary, pluvial events, refugia, relict populations, rodent middens.

*Correspondence: Claudio Latorre, Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile.
E-mail: clatorre@bio.puc.cl

INTRODUCTION

Assessing the consequences for biodiversity of current and future climate change is a multifaceted and complex challenge (Naeem *et al.*, 2012). Among other aspects, it must consider the responses of individual species (Engel *et al.*, 2011), interactions of climate change effects with other biotic

factors (Hof *et al.*, 2012) and uncertainties about the degree, rate and nature of projected future climate change. By providing evidence for how species have responded to past climate change, including by migration, habitat shifts, regional extirpation or even extinction, palaeoecological records help constrain the uncertainty of response times to a determined rate and direction of change (Dawson *et al.*, 2011; Seddon

et al., 2014). Past species distribution data can be used to identify priority conservation areas and help establish which species to protect (van Leeuwen *et al.*, 2008; Chambers *et al.*, 2013) as well as aiding in designing ecosystem management policies (Hallett & Walker, 2000; Gillson & Duffin, 2007; Lindbladh *et al.*, 2007).

Arid regions cover more than a third of the planet and are very sensitive to climate change (Holmgren *et al.*, 2006; Jiménez *et al.*, 2011). Variations in rainfall and temperature are not uncommon and can drive large swings in productivity on interannual time-scales (Noy-Meir, 1973). Many deserts around the world often experience flower blooms that are provoked by the response of annuals to large but infrequent rainfall events, such as those triggered by El Niño–Southern Oscillation (ENSO) (Gutiérrez *et al.*, 2000; Holmgren *et al.*, 2001a; Bowers, 2005). Intense drought can induce massive die-offs of perennial vegetation, often resetting demographic clocks in populations (Swetnam & Betancourt, 1998; Allen *et al.*, 2010).

In the arid central Andes and the adjacent Atacama Desert, precipitation variability has had a strong impact on the availability of water resources for various ecosystems at different time-scales (Latorre *et al.*, 2002, 2003; Nester *et al.*, 2007; Quade *et al.*, 2008). During the last glacial–interglacial transition at the end of the Pleistocene, the Central Andean Pluvial Event (CAPE) (Latorre *et al.*, 2006; Quade *et al.*, 2008; Placzek *et al.*, 2009) profoundly altered the distributions of many plant species in northern Chile (Latorre *et al.*, 2006). Rodent midden records from the central Atacama (22–24° S) have documented important elevational (c. 1000 m downslope) displacements of high Andean steppe grasses during the CAPE (Latorre *et al.*, 2002, 2003, 2006). These pluvial events have been shown to facilitate the dispersal and migration of species from higher vegetation belts into the lower desert (Latorre *et al.*, 2002; Díaz *et al.*, 2012).

Climate and vegetation change in northernmost Chile over the last 3000 years have been reconstructed using rodent middens (Holmgren *et al.*, 2008), plant macrofossils (Nester *et al.*, 2007; Gayo *et al.*, 2012), lake records (Valero-Garcés *et al.*, 2003; Moreno *et al.*, 2009) and tree-ring chronologies obtained from *Polylepis tarapacana* (Rosaceae) (Morales *et al.*, 2012). The latter display a strong ENSO signal (reconstructed summer rainfall anomalies) over the last 700 years, with wet years corresponding to La Niña and droughts to El Niño (Morales *et al.*, 2012). Furthermore, these records show a major centennial-scale trend towards more arid conditions that started in the 1930s and has continued until the present day (Morales *et al.*, 2012). The impact, however, of these recent climate changes on the vegetation and human societies of northernmost Chile has not been explored.

Pluvial events, refugia and relicts

Large-scale climate fluctuations associated with glacial–interglacial cycles are known to have affected the spatial distribution and ranges of many aridland plant species (Lyford

et al., 2003; Díaz *et al.*, 2012). The consequences range from species expansion during wet events to major range contraction and even extirpations during severe droughts (Jackson *et al.*, 2009). Pluvial events can also facilitate recruitment and augment population growth (Swetnam & Betancourt, 1998). In contrast, drought can cause massive die-offs, forming ‘relict’ or ‘ghost’ populations, which are often important components of regional biodiversity (Hampe & Jump, 2011).

Refugia are likely to have facilitated the maintenance of biodiversity over millennia and under changing climates (Gavin *et al.*, 2012). The concept of a refugium remains, however, controversial and there is no standard definition (Keppel *et al.*, 2011). We use the term as an area in which populations survive during periods of environmental stress (Hampe & Jump, 2011). Hence, a species that was widespread in the past, but now persists in a much smaller climatically favourable area, would constitute a refugial population.

To further our understanding of plant biogeography and its relationships with past climate change in the Atacama Desert, we present a new rodent midden record that spans more than 40,000 years. These samples were collected at Quebrada La Higuera (QLH) in the precordillera of the western Andes (Fig. 1) along two elevational bands. Rodent middens have been previously reported here (Holmgren *et al.*, 2001b, 2008), but the QLH midden record is the only record from this region with late Pleistocene middens, and is key for understanding how plant species responded to the end of the last glacial cycle. We use midden pollen, plant macrofossil evidence and chinchilla rat (*Abrocoma cinerea*) pellet diameters (a proxy for body size; see Smith *et al.*, 1995; Latorre *et al.*, 2010) to infer past environmental and vegetation change.

MATERIALS AND METHODS

Physical setting

Quebrada La Higuera (18.44° S; 69.72° W) is a narrow east–west-trending canyon that drains the western Andean precordillera in the northern Atacama Desert between 3000 and 3590 m above mean sea level (m a.s.l.) (Fig. 1). QLH has an intermittent stream flow with several smaller tributary watersheds that lie along the transition from the drier prepuna (mean annual rainfall of 60–80 mm yr⁻¹; see ‘Vegetation’) to the wetter puna (100–150 mm yr⁻¹ rainfall, mostly during the summer months; Garreaud *et al.*, 2003). The present mean annual temperature in the study area at 3100 m a.s.l. is c. 9 °C.

Vegetation

Owing to the strong north–south and east–west climate gradients, the vegetation of QLH displays marked latitudinal and elevational zonation (see Appendix S1 in Supporting Information). The four main zones or ‘bands’ are the coastal

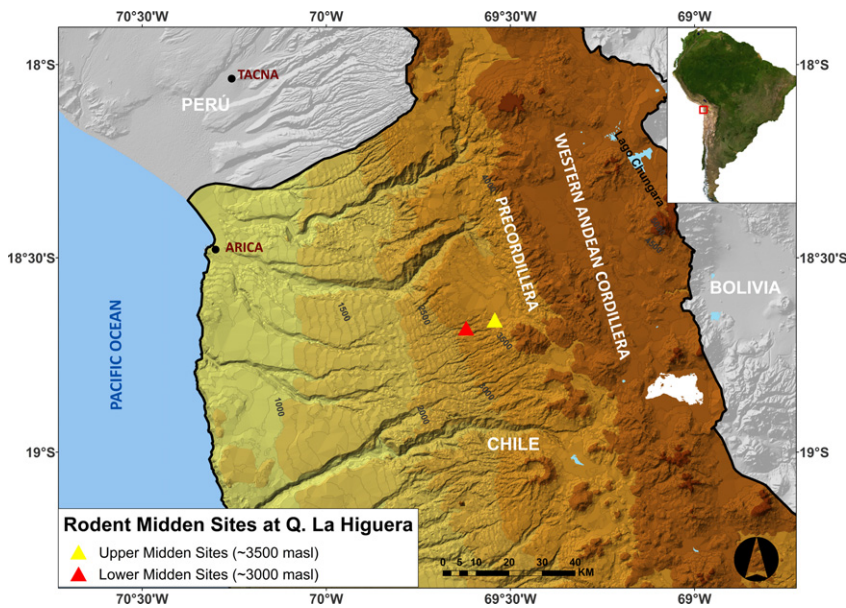


Figure 1 Regional map of the study area indicating the location of Quebrada La Higuera (QLH) in the Atacama Desert, northern Chile. The rodent midden localities described in this study are indicated by triangles. Colours change every 1000 m of elevation. Other relevant sites discussed here are also indicated (m a.s.l. = metres above sea level).

lomas, prepuna, tolar (or puna) and the high Andean steppe (Villagrán *et al.*, 1982; Arroyo *et al.*, 1988; Holmgren *et al.*, 2008). Most plant species in northern Chile are limited by low temperatures along their upper range, and by rainfall along their lower range (Latorre *et al.*, 2006). ‘Absolute desert’ – where plants are practically absent from the landscape – ranges from the coastal lomas up to the prepuna along the western Andean slope (see Appendix S1).

We collected middens from the prepuna (3000 m a.s.l.) and puna (3400 m a.s.l.) bands in QLH. Here, prepuna vegetation occurs above 2500 m a.s.l. and consists mostly of widely spaced xerophytic plants; it is characterized by the shrubs *Atriplex imbricata*, *Ambrosia artemisioides* and *Ephedra breana*, the cacti *Browningia candelaris*, *Cumulopuntia sphaerica* and *Corryocactus brevistylus*, and many summer annuals and grasses such as *Calandrinia*, *Lepidium*, *Cistanthe* and *Stipa annua*. The diverse puna (or tolar) band occurs between 3400 and 4000 m a.s.l., and includes the shrubs *Fabiana ramulosa*, *Diplostephium meyenii*, *Baccharis tola* and *Parastrephia quadrangularis*. Bunchgrasses and cushion plants appear in the transition between puna and high Andean steppe, dominated by Asteraceae shrubs (*Baccharis*, *Chuquiraga* and *Parastrephia*). The high Andean steppe occurs above 4000 m a.s.l. and is typically dominated at these latitudes by bunchgrasses of the genera *Festuca*, *Nassella* and *Deyeuxia*, and the cushion plants *Azorella compacta* and *Pycnophyllum molle* (Holmgren *et al.*, 2008). A local spring with abundant wetland vegetation outcrops along the valley floor near our higher-elevation site (see also Santoro *et al.*, 2011).

Field and laboratory methods

Rodent middens are discontinuous accumulations of organic debris (faeces, bones, and the remains of plants and insects) encased in hardened urine (amberat), and commonly found

in rock shelters, caves and crevices in the American aridlands, including the Atacama Desert (Latorre *et al.*, 2002, 2003). Fossil rodent middens represent individual snapshots of vegetation that must be compiled into chronological series for any particular site or area. We collected 30 fossil rodent middens from QLH; 15 middens were collected from 3050 to 3130 m a.s.l. and another 15 from 3230 to 3580 m a.s.l. (Fig. 1). Middens were extracted using a hammer and chisel, cleaned in the field for weathering rinds and surface contaminants, and split along clear stratigraphical units when recognizable. The midden-building agents were also identified in the field whenever possible.

Middens were processed in the lab following established procedures (Spaulding *et al.*, 1990; Latorre *et al.*, 2002). Approximately 100 mg of rodent faecal pellets from 22 middens (selected previously for their abundant macrofossils) were submitted for accelerator mass spectrometry (AMS) radiocarbon dating at the Keck Facility, University of California, Irvine. All dates were calibrated to calendar years before 1950 (or BP; Hogg *et al.*, 2013).

Macrofossils (plants, faecal pellets, bones and insects) were processed using standard techniques (Spaulding *et al.*, 1990; Latorre *et al.*, 2002). Plant macrofossils, including seeds, leaves, flowers and fruits, were quantified using a relative abundance scale (0, absent; 1, very rare; 2, rare; 3, common; 4, abundant; 5, dominant), and identified by comparison to a reference collection at the Departamento de Ecología, Pontificia Universidad Católica de Chile. Midden floras were classified by physiognomic affinity (prepuna, puna or steppe), and also as local or extralocal species by comparing the presence/absence of a species to the regional flora (Marticorena *et al.*, 1998) and with plant species present in modern middens.

Pollen extraction followed methods described for rodent middens in Maldonado *et al.* (2005). Pollen was extracted from fossil amberat using standard techniques (Faegri &

Iversen, 1989) and identified to the lowest taxonomic level possible using a reference collection located at the CEAZA, Universidad de La Serena. Each sample included a minimum pollen sum of 300 grains.

Woodrat (*Neotoma cinerea*) pellet diameters in packrat middens from south-western USA have been used to track rodent body-size fluctuations over time and have also been linked to past climate change, specifically summer temperatures (Smith *et al.*, 1995). In contrast, ashy chinchilla rat (*Abrocoma cinerea*) pellet diameters show a significant correlation with mean annual rainfall in modern middens, indicating that local productivity may be more important (Latorre *et al.*, 2010, 2013). For each midden, *Abrocoma* pellets were measured using a digital caliper (± 0.01 mm precision; Mitutoyo Sul Americana, São Paulo, Brazil) for approximately 200 selected pellets that were well preserved and relatively intact. The mean value of the largest 20% of these was then used as a proxy for the average value of the largest individuals in the population.

RESULTS

Radiocarbon dating

Radiocarbon ages reveal an uneven temporal coverage for the 22 middens selected (Table 1). The middens were clustered into three age groups: three middens dated to 38 ka or older, four middens dated from 14.42 to 11.47 ka, and the largest cluster (15 middens) dated from later than 610 cal. yr BP; almost all of these were collected between 3440 to 3575 m a.s.l. The other two midden clusters were collected at lower elevations in the prepuna (3050–3120 m a.s.l.). The two oldest middens (QLH85-1 and QLH85-2) are beyond the current calibration dataset SHCAL13, and were not calibrated.

Plant macrofossil and pollen assemblages

A total of 37 different plant taxa were identified to either genus or species from plant macrofossils (see Appendix S2). Macrofossil content and pollen descriptions follow the three different rodent midden age clusters (from oldest to youngest).

Midden cluster I (MC-I): > 49.7–38 ka

The two oldest middens of this cluster have a grassy texture with very few identifiable macrofossils. For example, we found only one *Ephedra* seed in the oldest midden (QLH85-1; > 49,700 ^{14}C yr BP), and the next midden in the sequence (QLH85-2; 47,200 ^{14}C yr BP) also contained few macrofossils, two of which were extralocal species found at higher elevations (by 200–500 m) than today: *Oreocereus leucotrichus* and *Parastrephia quadrangularis*. In contrast, the youngest midden (QLH185-A2; 37.4 ka) had a much greater diversity of plant macrofossils. Many of these were extralocal taxa found today at higher elevations (*Parastrephia quadrangularis*, *Baccharis tola*, *Phacelia* sp.) (Fig. 2a).

In contrast to the plant macrofossils, pollen is abundant in all these middens. The oldest midden was dominated by Ledocarpaceae type *Balbisia* and Asteraceae aff. *Baccharis* pollen – taxa found today some 300–400 m higher. Prepuna taxa (Ephedraceae, Asteraceae aff. *Senecio* and Boraginaceae) were also common; other pollen types (Polypodiaceae, Solanaceae aff. *Fabiana*, Solanaceae, Poaceae, Brassicaceae and Amaranthaceae) were much less frequent. As with the plant macrofossils, the youngest midden of the cluster showed considerably greater richness and changes in relative abundance as Ledocarpaceae type *Balbisia* decreased and Asteraceae aff. *Senecio* increased. In addition, new taxa also appeared (Fabaceae and Mimosaceae aff. *Prosopis*), whereas the pollen percentages of Ephedraceae, Polypodiaceae and Poaceae dropped off significantly (Fig. 2b). All these taxa (especially Poaceae) occur in the puna belt today.

Midden cluster II (MC-II): 14.4–11.5 ka

The four middens of this cluster had abundant plant macrofossils and many of these are indicative of the presence of extralocal species. *Cumulopuntia boliviana* (found in three middens) and *Solanum* sp. (two middens) are characteristic of the puna, and when present occurred at high relative abundances. Another extralocal species, *Oreocereus leucotrichus* (now found 300 m further up the valley), occurred in one of these middens. Local species such as *Browningia candelaris* and the riparian grass *Nassella pubiflora* also exhibited high relative abundances (Fig. 3a). A midden dated to 610 cal. yr BP (AD 1340) collected at the same lower-elevation site, is plotted here as a ‘modern’ analogue and serves as a comparison to the middens of this cluster.

Pollen results show that these middens were dominated by puna taxa, including Solanaceae aff. *Fabiana* and Asteraceae aff. *Baccharis*. Malvaceae and Polypodiaceae pollen, both characteristic of the puna belt, were also abundant in the three oldest middens, whereas the youngest midden (11.49 ka) had lower percentages of these taxa. Instead, the prepuna taxa Aizoaceae aff. *Tetragonia* and Caryophyllaceae, which appeared 12.41 ka, were more common. Portulacaceae aff. *Calandrinia*, Fabaceae, Asteraceae aff. *Chaetanthera* and Cactaceae aff. *Oreocereus* also appeared at 11.49 ka, showing that more prepuna elements were present in this assemblage. Other taxa, including Cactaceae indet. and Boraginaceae, were only present in the c. 14.42-ka midden, and then disappeared (Fig. 3b). Our ‘modern analogue’ midden (610 cal. yr BP) had a prepuna assemblage dominated by Amaranthaceae with the presence of Asteraceae *Ambrosia* type and Boraginaceae, all of which are also found at the site today.

Midden cluster III (MC-III): 610–0 cal. yr BP (AD 1340–1950)

This was the largest cluster, with 15 middens, all collected from our higher-elevation site. Rich in plant macrofossils,

Table 1 Collection data and radiocarbon chronology for the 22 middens from Quebrada La Higuera (QLH) in the Atacama Desert, northern Chile. Ages marked with an asterisk were beyond the calibration dataset.

Midden collection number	Elevation (m)	Slope aspect	Radiocarbon lab. no.	¹⁴ C age	SD	Median probability (cal. yr BP)	95% range (cal. yr BP)		yr AD	Material dated	No. identified plant taxa
							Lower	Upper			
QLH285	3457	SW	UCIAMS-73918	30	15	-6	-7	0*	1950	<i>Abrocoma</i> pellets	13
QLH281	3454	SW	UCIAMS-73917	85	15	50	-7	135	1900	<i>Abrocoma</i> pellets	4
QLH86	3459	S	UCIAMS-73925	105	15	55	-6	241	1895	<i>Abrocoma</i> pellets	7
QLH182-A	3469	NNW	UCIAMS-73919	110	15	60	-6	242	1890	<i>Abrocoma</i> pellets	11
QLH182-B	3469	NNW	UCIAMS-73920	120	20	80	1	251	1870	<i>Abrocoma</i> pellets	13
QLH183	3468	N	UCIAMS-73915	140	15	90	1	253	1860	<i>Abrocoma</i> pellets	16
QLH287	3446	SE	UCIAMS-73914	175	15	145	1	277	1805	<i>Abrocoma</i> pellets	13
QLH279	3469	—	UCIAMS-73926	215	15	190	148	285	1760	<i>Abrocoma</i> pellets	12
QLH280	3458	SW	UCIAMS-73916	285	15	300	160	321	1650	<i>Abrocoma</i> pellets	11
QLH99	3455	SE	UCIAMS-73923	305	15	310	289	438	1640	<i>Abrocoma</i> pellets	11
QLH289	3439	S	UCIAMS-73922	390	20	385	326	489	1565	<i>Abrocoma</i> pellets	3
QLH271	3471	NW	UCIAMS-73927	585	15	545	526	555	1405	<i>Abrocoma</i> pellets	18
QLH282	3461	SW	UCIAMS-73921	620	15	560	542	629	1390	<i>Abrocoma</i> pellets	16
QLH184	3576	S	UCIAMS-73924	650	15	610	552	636	1340	<i>Abrocoma</i> pellets	13
QLH371c	3055	S	UCIAMS-73928	660	15	610	554	645	1340	<i>Abrocoma</i> pellets	10
QLH182B2-3	3082	S	UCIAMS-73932	10,055	25	11,490	11,315	11,703	—	<i>Phyllotis</i> pellets	11
QLH182B2-2	3082	S	UCIAMS-73931	10,500	25	12,410	12,114	12,548	—	<i>Phyllotis</i> pellets	7
QLH185B-1	3082	S	UCIAMS-73929	12,321	25	14,170	14,029	14,350	—	<i>Phyllotis</i> pellets	5
QLH185B2-1	3082	S	UCIAMS-73930	12,390	25	14,320	14,122	14,643	—	<i>Phyllotis</i> pellets	8
QLH185A-2	3082	S	UCIAMS-73934	33,260	270	37,440	36,576	38,319	—	<i>Phyllotis</i> pellets	13
QLH85-2	3126	SW	UCIAMS-73913	47,200	1500	*	*	*	—	<i>Phyllotis</i> pellets	3
QLH85-1	3126	SE	UCIAMS-73933	> 49,700	—	*	*	*	—	<i>Phyllotis</i> pellets	1

these averaged 11 identified taxa per midden. A considerable number of taxa occurred consistently throughout the record, such as *Allionia incarnata*, *Cristaria* spp., *Baccharis tola*, *Scirpus* sp. and *Nassella pubiflora*. Other taxa were present in high abundances in the oldest middens (c. 610–560 cal. yr BP), disappeared afterwards (c. 545 cal. yr BP) and then reappeared at c. 190 yr; examples include the cacti *Oreocereus hempeianus* and *Oreocereus leucotrichus*, the prepuna shrub *Ambrosia artemisioides*, perennial plants such as *Chenopodium* sp., *Ephedra breana* and the annual *Heterosperma* sp. An important pattern of turnover occurred among the summer annuals and grasses in this cluster: *Cistanthe* spp., *Aristida adscensionis*, *Tagetes multiflora* and *Euphorbia* sp. all occurred in the oldest midden (c. 610–560 cal. yr BP) but were not found in the youngest middens. Instead, other annuals such as *Sisymbrium* sp. appeared at 145 cal. yr BP (Fig. 4a).

Midden pollen revealed a rich assemblage. Asteraceae aff. *Baccharis*, Asteraceae aff. *Senecio*, and Ledocarpaceae were all dominant, and Boraginaceae, Solanaceae aff. *Solanum*, Asteraceae aff. *Ambrosia*, *Ephedra* and Fabaceae also occurred in lower percentages. The puna shrub Asteraceae aff. *Baccharis* was more abundant at 400–300 cal. yr BP together with low percentages of other taxa, suggesting an impoverished puna assemblage. Asteraceae aff. *Parastrephia*, a puna shrub found today above 3700 m a.s.l., appeared abruptly at c. 190 cal. yr BP (AD 1760), and increased remarkably in abundance until the most recent middens, which had decreased percentages of this taxon (Figs 4b & 5a).

Variations in *Abrocoma cinerea* pellet diameters

Only MC-III had *A. cinerea* middens for which pellets could be measured (the older middens were all built by *Phyllotis* spp.) (Table 1). Within MC-III (610 cal. yr BP to present), four major trends in average pellet diameters are readily apparent (Fig. 5b): (1) a decrease in diameters occurred from 610 to 545 cal. yr BP (AD 1340–1405), (2) pellet diameters increased in size until 300 cal. yr BP (AD 1650), followed by (3) a strong reduction in diameters at 190 cal. yr BP (AD 1760), which in turn gave way to (4) an almost 75% increase in pellet diameters, reaching maximum pellet diameters at 145 cal. yr BP (AD 1805). A slow but steady decrease in pellet diameters occurred across the median age probability of middens over the last 150 years – the trend is apparent despite the large errors typical of very young (within the last 200 years) calibrated ¹⁴C ages (Fig. 5b).

DISCUSSION

Late Quaternary vegetation and climate change in the northern Atacama

Midden-building rodents in the Atacama appear to be generalists, and their middens are therefore representative samples of the surrounding local vegetation (Cortés *et al.*, 2002; Latorre *et al.*, 2003; Salinas & Latorre, 2007). Past local climate and vegetation change can thus be garnered by establishing the presence of extralocals and their physiognomic

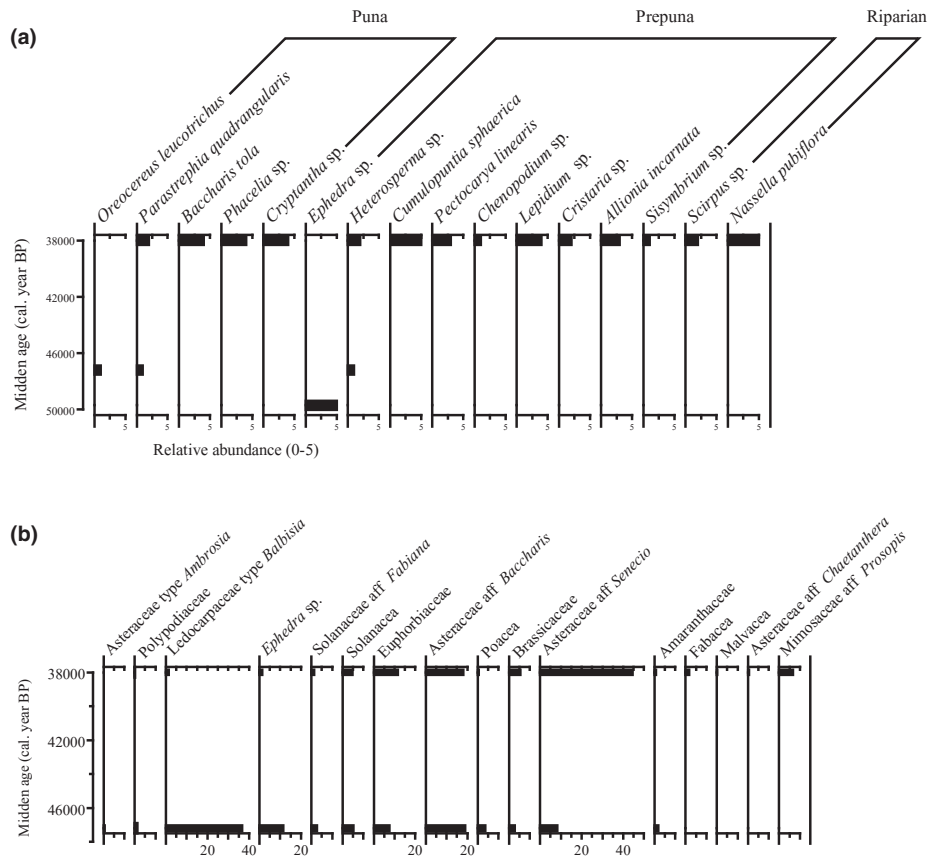


Figure 2 Midden cluster I (MC-I) (older than 37 ka, c. 3100 m a.s.l., three middens) from Quebrada La Higuera in the Atacama Desert, northern Chile. (a) Plant macrofossil diagram. Relative abundance index runs from 0 (absent) to 5 (dominant). Note the sparse taxa in older middens. (b) Pollen percentage diagram for two middens from this cluster. The total pollen sum for each sample included a minimum of 300 grain counts.

and phytogeographical affinities. In part, this relies on the distribution of vascular plant species in northern Chile and the associated climatic gradients (Villagrán *et al.*, 1982; Arroyo *et al.*, 1988; Latorre *et al.*, 2003, 2006). Elevated macrofossil richness and elevated relative abundances of species that today grow at higher elevations, including *Cryptantha* sp., *Oreocereus leucotrichus*, *Parastrephia quadrangularis*, *Baccharis tola* and other taxa, occur in the oldest midden cluster (MC-I). Given the elevation (3050 m) at which these middens were collected, the presence of these species evinces important changes in Andean biogeography, especially at 37 ka (see next section). The higher moisture requirement of these plants ($> 60 \text{ mm yr}^{-1}$, compared to the c. 30 mm yr^{-1} at these sites today) is likely to indicate that their dispersal into the lower prepuna was facilitated by sustained increases in local summer rainfall. Something similar occurs for MC-II, where the elevated species richness in middens and the presence of extralocals such as *Cumulopuntia boliviana*, *Oreocereus leucotrichus* and *Solanum* sp. reveal important increases in past local rainfall from 14.4 to 11.5 ka.

Midden pollen also reveals the presence of extralocal taxa found today at higher elevations. The oldest cluster (MC-I) is dominated by pollen from the puna-extralocal Asteraceae

aff. *Baccharis*. For MC-II, the extralocal species *Solanaceae* aff. *Fabiana* and *Asteraceae* aff. *Baccharis* are also indicative of wetter conditions. These midden clusters show major changes in the distribution of plant species at QLH, which in turn reflect important hydrological changes during periods of increased rainfall (pluvial events). For MC-II, these changes are also synchronous for the most part with the widespread CAPE.

Palaeoecological and societal evidence for a recent pluvial in historical times

Rodent midden series are not typically used as high-resolution records of past climate change because they are discrete, non-continuous units and the duration of a depositional episode is often unknown. Hence, their use on more recent time-scales (the last 1000 years) is rarely explored. Some of these limitations can be overcome, however, by referring to different proxies from a single given midden, as each reflects different aspects of past environmental change.

The midden pollen record shows major changes in certain extralocal taxa in MC-III. In contrast to the plant macrofossils, midden pollen is not a measure of plant species presence

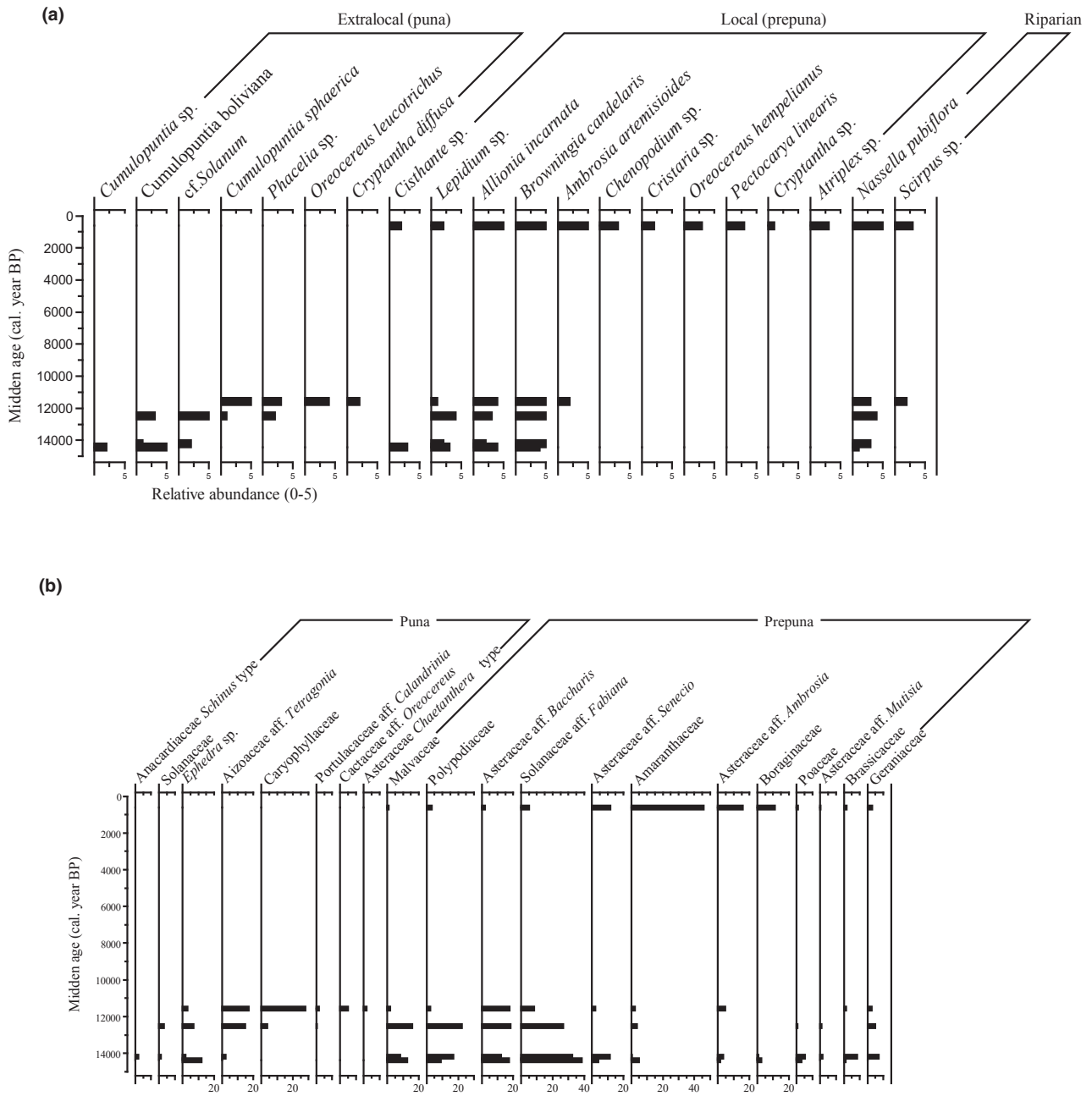


Figure 3 Midden cluster II (MC-II) series (14.4–11.5 ka, c. 3080 m a.s.l., four middens) from Quebrada La Higuera in the Atacama Desert, northern Chile. (a) Plant macrofossil diagram. Relative abundance index runs from 0 (absent) to 5 (dominant). (b) Midden pollen percentage diagram based on three middens from this cluster. The total pollen sum for each sample included a minimum of 300 grain counts. Note the large break in ages between late Pleistocene middens and a ‘modern’ midden (QLH371c, 610 cal. yr BP) collected at the same site for comparisons.

or absence but of abundance, and can often complement the macrofossil record (Maldonado *et al.*, 2005; Díaz *et al.*, 2012). Thus, Asteraceae aff. *Baccharis* pollen was abundant until AD 1650 and then decreased, possibly because of increasing drought. A large increase in Asteraceae aff. *Parastrephia* pollen beginning in AD 1760 reflects an increase in rainfall: this puna shrub is now found c. 200–300 m further upslope (Fig. 5a). This historical pluvial event is also docu-

mented in the *Polylepis* tree-ring chronology from the western Altiplano (Morales *et al.*, 2012; plotted in Fig. 5c) and the Lago Chungará record, which indicates wetter conditions towards the end of the 1800s (Valero-Garcés *et al.*, 2003).

Large changes occurred in *A. cinerea* pellet diameters since 610 cal. yr BP (AD 1340 onwards; Fig. 5b). Pellet diameters oscillated around low average values during the earlier part of the record, reaching a minimum at AD 1805. These values

then increased and remained high until *c.* AD 1900 (calibration errors increase for younger ^{14}C dates), after which the diameters decreased towards modern values. If these values (through changes in rodent body size) reflect mean annual rainfall as has been previously hypothesized (Latorre *et al.*, 2010, 2013), then as with the increase in Asteraceae aff. *Parastrephia* pollen, these trends are indicative of a large pluvial event during the first half of the 1800s. They could also be indicative of cooler temperatures (indicated by larger body sizes), but this interpretation would contradict other regional evidence that points to increased warming at this time (Rabatel *et al.*, 2008).

The midden macrofossils identified in MC-III are complicated to interpret. Assemblages characterized by *Chenopodium* sp., *Nassella pubiflora*, *Scirpus* sp., *Allionia incarnata*, *Cryptantha* sp. and *Cristaria* spp. are all local. An important turnover among annuals occurred from AD 1405 to 1650, as *Sisymbrium* appeared in the record and *Aristida adscensionis* and *Tagetes multiflora* (both summer annuals) disappeared. Such 'stochastic stability' appears to be comparable with a recent midden study that showed similar stability over the last 3000 years in northernmost Chile (Holmgren *et al.*, 2008).

We speculate that this apparent 'stochastic stability' in our recent midden macrofloras is perhaps due to current floristic spatial heterogeneity. The youngest middens were often dominated by plants currently growing next to the collection site. The implication is that any changes in plant species assemblages and especially perennials recorded in middens at these small temporal/spatial scales could be unrelated to changes to regional climate. This is in contrast to the midden pollen record, which clearly indicates the persistent presence of a particular pollen type (*i.e.* *Parastrephia*) starting in AD 1760. There are many vectors for pollen in middens (Díaz *et al.*, 2012), but the fact that this pollen type is absent from older middens in MC-III supports our interpretation that it must be locally derived (if this pollen were wind-dispersed, it would probably show up in small amounts in all the middens). Furthermore, this trend resembles the changes in *Abrocoma cinerea* pellet diameters measured in these same middens. We conclude that if the spatial variation in vegetation between midden sites is larger than the possible vegetation response to a short-lived pluvial event (*i.e.* one that lasts several decades), then such events may not be reflected in midden macrofloras, which would instead produce a record of apparent 'stability' or stochastic changes.

Further evidence and impacts of a recent 'historical Andean pluvial' come from local accounts, archaeological and historical records, as all suggest there were important shifts in human activities, including farming, plant collection, seasonal pastoralism and even hunting (Núñez, 1986; Núñez *et al.*, 2010). Historical demographic data show a past 'bonanza epoch' during the early-to-mid 1800s, with a gradual increase in the indigenous Aymara population of the Tarapacá region during the 1700s, followed by an abrupt decline after 1850 (Larraín, 1974; van Kessel, 1991; Gaete,

2006) (Fig. 5d). This 'bonanza' and subsequent collapse are still in the oral tradition of the peoples from the Arica and Tarapacá highlands (C.M.S., unpubl. obs.). With few exceptions (Larraín, 1974; Núñez, 1986; Gaete, 2006), the historical and archaeological arguments used to explain these demographic changes focus on urban expansion, development of the nitrate industry and the enforcement of new geopolitical boundaries and policies after the War of the Pacific (between Chile, Peru and Bolivia in the late 1800s), or even the aftermath of epidemics (Larraín, 1974; van Kessel, 1991; Gaete, 2006; Castro, 2008; González, 2009; González *et al.*, 2014).

We suggest that a major pluvial event, followed by sustained centennial-scale drought, would have played a major role in the increased population and subsequent depopulation of these rural areas. As the climate became drier and plant resources succumbed to drought, pastoralism, farming and hunting are likely to have shifted from a permanent to a more intermittent habitation system. People would thus have migrated from their homelands in the prepuna as life became harsher through the increasing aridity. They went on to create a surge of highland migrants that supplied cheap labour for the (now also abandoned) nitrate mining camps and towns in the lower Atacama Desert, as well as populating the emergent coastal cities of Arica and Iquique.

Modern-day refugia and relict populations in the Atacama: implications for conservation in a changing climate

One of the most salient features of the middens from the MC-I and MC-II clusters is the presence of extralocal species such as *Baccharis tola*, *Cumulopuntia boliviana* and *Oreocereus leucotrichus*. The distribution of these species is limited by rainfall and they are currently restricted to high-elevation puna habitats (Latorre *et al.*, 2006). As with other midden records from the central Atacama, these show that, during the late Pleistocene, the low-elevation prepuna vegetation was enriched by puna plant species but the more aridity-tolerant species were still present (*i.e.* *Browningia candelaris*, *Allionia incarnata*, *Lepidium* and *Cistanthe*).

We suggest that these results imply that much of the central Andes and Altiplano are modern-day refugia for many species found here and nowhere else. Such elevations would rarely have been occupied by these same species during the colder periods of the Pleistocene, and in fact pollen from lakes and other records in the western Altiplano indicate that very little vegetation was present during extreme cold phases such as the Last Glacial Maximum (Grosjean *et al.*, 2001; Paduano *et al.*, 2003; Maldonado *et al.*, 2005). Thus, many high-Andean plant species would have been completely absent from the Altiplano during colder periods (*i.e.* most of a glacial period), only returning to the region at the beginning of warmer interglacials.

Another important result of this study is that the lower elevations of the western Andean prepuna appear to be

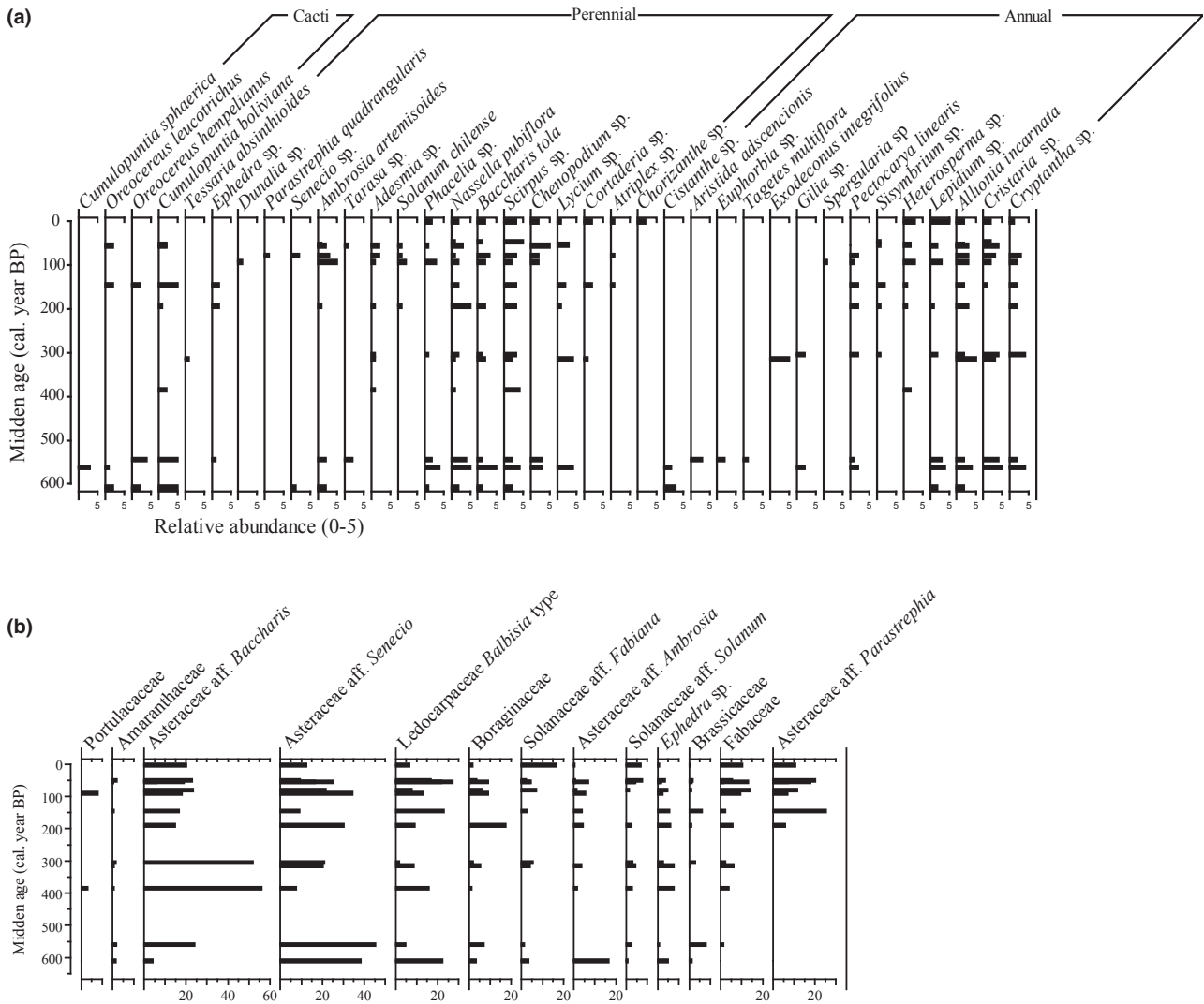


Figure 4 Midden cluster III (MC-III) series (the last 610 yr cal. BP, c. 3500 m, 14 middens) from Quebrada La Higuera in the Atacama Desert, northern Chile. (a) Plant macrofossil diagram (14 middens). Relative abundance was estimated by using a relative abundance index (where 0 is absent and 5 dominant). (b) Midden pollen percentage diagram based on 11 middens from this cluster. The total pollen sum for each sample included a minimum of 300 grain counts. Note the presence of *Asteraceae* aff. *Parastrephia* pollen type (a shrub not found at the site and currently growing at higher elevations) starting at 200 cal. yr BP.

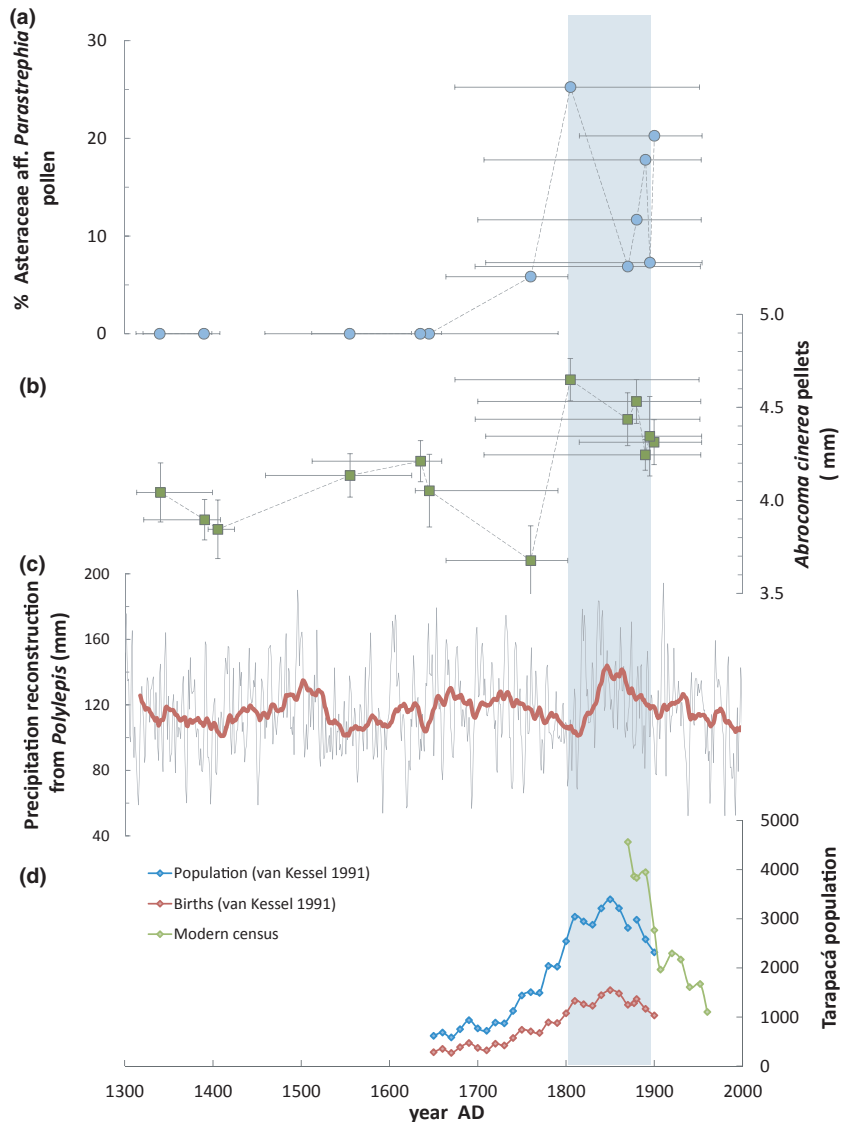
‘relict’ landscapes, the product of long-term swings in natural climate variability in which several decades of wetter climate are followed by many decades of drought. Today, many large, dead-standing columnar cacti can be seen, as can the lack of population rejuvenation in the lower portion of the QLH watershed. This was recently quantified by Pinto & Kirberg (2009), who used first-hand observations to evaluate the status of two northern Atacama cacti (*Browningia candelaris* and *Corryocactus brevistylus*). They found high mortality in populations of both species in the lower prepuna (2400–2800 m a.s.l.) (see Appendix S1).

Such mass mortality in cacti due to drought is not uncommon. Extensive saguaro (*Carnegiea gigantea*) cactus populations in the eastern Saguaro National Monument (near Tucson, AZ) that were established during wetter periods in

the late 1700s and early 1800s are now suffering major die-backs due to sustained drought (Pierson *et al.*, 2013). Similarly, we relate mortality in northern Chile cactus populations to decreasing regional rainfall since the early 1900s and possibly even earlier (Gaete, 2006). Intense pluvial events followed by extended droughts are typical of desert environments, and can reset the demographic clocks of an important portion of its perennial flora (Swetnam & Betancourt, 1998), shaping landscapes that are then a result of past climate change.

Given the nature of past climate and vegetation changes at QLH, we point out two aspects that have implications for future conservation efforts of these unique floras. First, the central Andes and Altiplano are very likely to be modern-day refugia for many plant species that may have had much

Figure 5 Proxies for past climate change over the last c. 700 years for the northern Atacama Desert (a–b) and the western Altiplano (c), as well as human demographic changes in the Andean precordillera of northern Chile (d). The most recent ‘historical’ pluvial is indicated with blue shading. (a) Percentage changes in Asteraceae aff. *Parastrephia* pollen type as measured from middens collected from the higher elevation site within Quebrada La Higuera (QLH) (see Fig. 3b). Horizontal error bars represent calibrated ^{14}C ages at 95% ranges. The dashed line is shown for the purposes of illustrating major trends and is not meant to imply that middens are continuous records. (b) Changes in the average top 20% of *Abrocoma cinerea* pellet diameters for the same QLH middens. Vertical bars are one standard deviation for pellet diameter measurements and horizontal error bars as in panel (a). (c) A tree-ring reconstruction of annual precipitation using *Polylepis* (Rosaceae) trees from the western Altiplano for the period AD 1300–2000 (annual precipitation expressed as percentages of the 1982–2000 instrumental precipitation mean). The red line is a 30-year moving average (modified from Morales *et al.*, 2012). (d) Census data from several sources showing major population trends for the inland villages of the Tarapacá region (or province depending on how far back the data were taken). Note that data are from different sources.



more extensive distributions at lower elevations in the past but are now restricted to very small or fragmented populations. Second, we point out the effects of recent climate change over the last few centuries has had on the prepuna vegetation of the western Andes. The large-scale vegetation dynamics alluded to here could be tested with population genetics, because several species could have both young (Holocene) populations in the Altiplano today and older pluvial relicts of diverse ages at lower elevations. These findings are also key for understanding the cultural, economic and demographic changes in human societies of northernmost Chile over the last two centuries.

Models of future climate change under scenarios of increased greenhouse gas concentrations indicate that aridity is expected to increase over the western Altiplano (Minvielle & Garreaud, 2011; Thibeault *et al.*, 2011). This is due to a simulated increase in upper-level westerly wind-flow, which blocks the advection of moisture-laden easterly air masses. Thus, the desert floras of northern Chile and the central

Andes face a very uncertain future. Efforts to conserve these ecosystems and communities should focus on the protection of refugia located in the western Altiplano, and towards mitigation strategies for the floras of the prepuna, especially of large perennial species. Similarly, the past and predicted future scenarios should be considered in future resource planning.

ACKNOWLEDGEMENTS

We thank M. Frugone, N. Villavicencio, K. Ojeda, P. Villegas, F. González, E. Gayó and F.P. Díaz for their help in the field. We thank H. Orellana for drafting Fig. 1. Comments by J. L. Betancourt, C. Holmgren and two anonymous referees helped to improve this manuscript significantly. Funding was provided by FONDECYT 1100916 (to C.L., A.M. and C.M.S.), FONDECYT 1130279 (to A.M.) and the Institute of Ecology and Biodiversity (grants ICM P05-002 and PFB 23).

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Arroyo, M.T.K., 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.
- Bowers, J.E. (2005) El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts. *Journal of the Torrey Botanical Society*, **132**, 38–49.
- Castro, L. (2008) El estado chileno, los agentes fiscales y el temprano ordenamiento administrativo del espacio andino de la provincia de Tarapacá (1880–1930) [The Chilean state, government agents, and the early administrative organization of the Andean space of the Province of Tarapacá (1880–1930)]. *Chungara Revista de Antropología Chilena*, **40**, 219–233 (in Spanish).
- Cortés, A., Rau, J.R., Miranda, E. & Jimenez, J.E. (2002) Food habits of *Lagidium viscacia* and *Abrocoma cinerea*: syntopic rodents in high Andean environments of northern Chile. *Revista Chilena de Historia Natural*, **75**, 583–593.
- Chambers, F.M., Cloutman, E.W., Daniell, J.R.G., Mauquoy, D. & Jones, P.S. (2013) Long-term ecological study (palaeoecology) to chronicle habitat degradation and inform conservation ecology: an exemplar from the Brecon Beacons, South Wales. *Biodiversity and Conservation*, **22**, 719–736.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.
- Díaz, F.P., Latorre, C., Maldonado, A., Quade, J. & Betancourt, J.L. (2012) Rodent middens reveal episodic, long-distance plant colonizations across the hyperarid Atacama Desert over the last 34,000 years. *Journal of Biogeography*, **39**, 510–525.
- Engel, K., Tollrian, R. & Jeschke, J.M. (2011) Integrating biological invasions, climate change and phenotypic plasticity. *Communicative and Integrative Biology*, **4**, 247–250.
- Faegri, K. & Iversen, J. (1989) *Textbook of pollen analysis*, 4th edn. Blackwell Science, Oxford.
- Gaete, A. (2006) Análisis y consecuencias del despoblamiento de comunidades del norte de Chile, con especial referencia a las hoyas hidrográficas de las quebradas de Aroma y Tarapacá (Pr. Región de Tarapacá. Chile) [Analysis and consequences of depopulation of communities in northern Chile, with special reference to the Aroma and Tarapacá hydrographical basins (Pr. Region Tarapacá. Chile)]. *Boletín de Geografía*, **24–25**, 3–19 (in Spanish).
- Garreaud, R., Vuille, M. & Clement, A.C. (2003) The climate of the Altiplano: observed current conditions and mechanisms of past changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194**, 5–22.
- Gavin, D.G., Dobrowski, S.Z., Hampe, A., Hu, F.S. & Rodriguez-Sanchez, F. (2012) Climate refugia: joint inference from fossils, genetics and models. *PAGES news*, **20**, 105.
- Gayo, E.M., Latorre, C., Jordan, T.E., Nester, P.L., Estay, S.A., Ojeda, K.F. & Santoro, C.M. (2012) Late Quaternary hydrological and ecological changes in the hyperarid core of the northern Atacama Desert (~21°S). *Earth-Science Reviews*, **113**, 120–140.
- Gillson, L. & Duffin, K.I. (2007) Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 309–319.
- González, S. (2009) La presencia boliviana en la sociedad del salitre y la nueva definición de la frontera: auge y caída de una dinámica transfronteriza (Tarapacá 1880–1930) [The Bolivian presence in the nitrate society and the new definition of the frontier: the rise and fall of a transborder dynamic (Tarapacá 1880–1930)]. *Chungara Revista de Antropología Chilena*, **41**, 71–81 (in Spanish).
- González, H., Gundermann, H. & Hidalgo, J. (2014) Comunidad indígena y construcción histórica del espacio entre los Aymara del norte de Chile [Indigenous communities and historical construction of space among the Aymara of northern Chile]. *Chungara, Revista de Antropología Chilena*, **46**, 233–246 (in Spanish).
- Grosjean, M., van Leeuwen, J.F.N., van der Knaap, W.O., Geyh, M.A., Ammann, B., Tanner, W., Messerli, B., Núñez, L.A., Valero-Garcés, B. & Veit, H. (2001) A 22,000 ¹⁴C yr BP sediment and pollen record of climate change from Laguna Miscanti (23°S), northern Chile. *Global and Planetary Change*, **28**, 35–51.
- Gutiérrez, J.R., Arancio, G. & Jaksic, F.M. (2000) Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. *Journal of Vegetation Science*, **11**, 641–648.
- Hallett, D.J. & Walker, R.C. (2000) Paleocology and its application to fire and vegetation management in Kootenay National Park, British Columbia. *Journal of Paleolimnology*, **24**, 401–414.
- Hampe, A. & Jump, A.S. (2011) Climatic relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 313–333.
- Hof, A.R., Jansson, R. & Nilsson, C. (2012) How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. *Diversity and Distributions*, **18**, 554–562.
- Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M. & Zimmerman, S.R.H. (2013) SHCal13 Southern Hemisphere calibration, 0–50,000 cal yr BP. *Radiocarbon*, **55**, 1889–1903.
- Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J.R. & Mohren, G.M.J. (2001a) El Niño effects on the dynamics of

- terrestrial ecosystems. *Trends in Ecology and Evolution*, **16**, 89–94.
- Holmgren, C.A., Betancourt, J.L., Rylander, K.A., Roque, J., Tovar, O., Zeballos, H., Linares, E. & Quade, J. (2001b) Holocene vegetation history from fossil rodent middens near Arequipa, Peru. *Quaternary Research*, **56**, 242–251.
- Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F.M., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtalli, M.A., Richter, M., Sabaté, S. & Squeo, F.A. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.
- Holmgren, C.A., Rosello, E., Latorre, C. & Betancourt, J.L. (2008) Late-Holocene fossil rodent middens from the Arica region of northernmost Chile. *Journal of Arid Environments*, **72**, 677–686.
- Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences USA*, **109**, 19685–19692.
- Jiménez, M.A., Jaksic, F.M., Armesto, J.J., Gaxiola, A., Meserve, P.L., Kelt, D.A. & Gutiérrez, J.R. (2011) Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecology Letters*, **14**, 1227–1235.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D. & Franklin, S.E. (2011) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, **21**, 393–404.
- van Kessel, J. (1991) Los Aymaras contemporáneos de Chile (1879–1990): su historia social [Contemporary Aymara of Chile (1879–1990): their social history]. *Diálogo Andino*, **10**, 47–72 (in Spanish).
- Larraín, H. (1974) Análisis de las causas de despoblamiento entre las comunidades indígenas del Norte de Chile, con especial referencia a las Hoyas hidrográficas de las Quebradas Aroma y Tarapacá. *Revista de Geografía Norte Grande*, **1**, 125–154.
- 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. & Arroyo, M.T.K. (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., González, F.J., Houston, J., Rojas, M. & Mujica, M.I. (2010) Reliable mean annual rainfall estimates using chinchilla rat (*Abrocoma*) middens from the Atacama Desert during the late Quaternary. Abstract PP2B-05. *AGU Meeting of the Americas, Foz do Iguaçu, Brazil, 8–12 August 2010*.
- Latorre, C., González, F.J., Rocuant, M.I., Houston, J. & Rojas, M. (2013) Millennial and sub-millennial scale variations in rainfall revealed by chinchilla rat (*Abrocoma*) middens over the last 16,400 years in the central Atacama Desert (22–24°S). *PAGES 4th Open Science Meeting, Goa, India, 13–16 February, 2013*.
- van Leeuwen, J.F.N., Froyd, C.A., van der Knaap, W.O., Coffey, E.E., Tye, A. & Willis, K.J. (2008) Fossil pollen as a guide to conservation in the Galápagos. *Science*, **322**, 1206.
- Lindbladh, M., Brunet, J., Hannon, G., Niklasson, M., Eliasson, P., Eriksson, G. & Ekstrand, A. (2007) Forest history as a basis for ecosystem restoration – a multidisciplinary case study in a south Swedish temperate landscape. *Restoration Ecology*, **15**, 284–295.
- Lyford, M.E., Jackson, S.T., Betancourt, J.L. & Gray, S.T. (2003) Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Monographs*, **73**, 567–583.
- 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.
- Martcorena, C., Matthei, O., Rodríguez, R., Arroyo, M.K., Muñoz, M., Squeo, F. & Arancio, G. (1998) Catálogo de la flora vascular de la Segunda Región (Región de Antofagasta), Chile [Catalogue of the vascular flora of the Second Region (Antofagasta), Chile]. *Gayana Botánica*, **55**, 23–83 (in Spanish).
- Minvielle, M. & Garreaud, R.D. (2011) Projecting rainfall changes over the South American Altiplano. *Journal of Climate*, **24**, 4577–4583.
- Morales, M.S., Christie, D.A., Villalba, R., Argollo, J., Pacajes, J., Silva, J.S., Alvarez, C.A., Llanabure, J.C. & Soliz Gamboa, C.C. (2012) Precipitation changes in the South American Altiplano since 1300 AD reconstructed by tree-rings. *Climate of the Past*, **8**, 653–666.
- Moreno, A., Santoro, C.M. & Latorre, C. (2009) Climate change and human occupation in the northernmost Chilean Altiplano over the last ca. 11 500 cal. a BP. *Journal of Quaternary Science*, **24**, 373–382.
- Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The functions of biological diversity in an age of extinction. *Science*, **336**, 1401–1406.
- Nester, P.L., Gayó, 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.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Núñez, L. (1986) The evolution of a valley: population resources of Tarapacá over a millennium. *Anthropological history of Andean polities* (ed. by J.V. Murra, N. Wachtel and J. Revel), pp. 23–34. Cambridge University Press, Cambridge, UK.
- Núñez, L., Grosjean, M. & Cartajena, I. (2010) Sequential analysis of human occupation patterns and resource use in

- the Atacama Desert. *Chungara Revista de Antropología Chilena*, **42**, 363–391.
- Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C. & Seltzer, G.O. (2003) A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194**, 259–279.
- Pierson, E.A., Turner, R.M. & Betancourt, J.L. (2013) Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert. *Journal of Arid Environments*, **88**, 57–69.
- Pinto, R. & Kirberg, A. (2009) *Cactus del extremo norte de Chile*. AMF, Santiago, Chile.
- 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.
- 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.
- Rabatel, A., Francou, B., Jomelli, V., Naveau, P. & Grancher, D. (2008) A chronology of the Little Ice Age in the tropical Andes of Bolivia (16°S) and its implications for climate reconstruction. *Quaternary Research*, **70**, 198–212.
- Salinas, M.E. & Latorre, C. (2007) Un estudio tafonómico sobre la representatividad de la diversidad de especies vegetales en paleomadrigueras de roedores del Norte de Chile. *III Reunión Binacional de Ecología, La Serena, 30 September – 4 October 2007*.
- Santoro, C.M., Ugalde, P.C., Latorre, C., Salas, C., Osorio, D., Jackson, D. & Gayó, E. (2011) Ocupación humana pleistocénica en el Desierto de Atacama: primeros resultados de la aplicación de un modelo predictivo de investigación interdisciplinaria [Pleistocene human occupation in the Atacama Desert: first results from the application of an interdisciplinary predictive research model]. *Chungara Revista de Antropología Chilena*, **43**, 353–366 (in Spanish).
- Seddon, A.W.R., Mackay, A.W., Baker, A.G. *et al.* (2014) Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology*, **102**, 256–267.
- Smith, F.A., Betancourt, J.L. & Brown, J.H. (1995) Evolution of body size in the woodrat over the past 25000 years of climate change. *Science*, **270**, 2012–2014.
- 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.
- Swetnam, T.W. & Betancourt, J.L. (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*, **11**, 3128–3147.
- Thibeault, J., Setha, A. & Wang, G.-L. (2011) Mechanisms of summertime precipitation variability in the Bolivian Altiplano: present and future. *International Journal of Climatology*, **32**, 2033–2041.
- Valero-Garcés, B.L., Delgado-Huertas, A., Navas, A., Edwards, L., Schwalb, A. & Ratto, N. (2003) Patterns of regional hydrological variability in central-southern Altiplano (18°–26°S) lakes during the last 500 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **194**, 319–338.
- Villagrán, C., Arroyo, M.T.K. & Armesto, J.J. (1982) La vegetación de un transecto altitudinal en los Andes del norte de Chile (18°–19°S) [The vegetation of an altitudinal transect in the Andes of northern Chile (18°–19°S)]. *El ambiente natural y las poblaciones humanas de los Andes de norte grande de Chile (Arica, lat. 18° 28' S)* (ed. by A. Veloso and E. Bustos), pp. 13–69. UNESCO, Santiago, Chile (in Spanish).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Schematic representations of the different vegetational bands at QLH (18° S), and photographs of rodent midden localities and of a standing, dead *Browningia candelaris* or ‘cactus candelabro’ in the lower prepuna of northernmost Chile.

Appendix S2 Taxonomic and associated phytogeographical data of the 37 plant macrofossil taxa identified from QLH rodent middens.

DATA ACCESSIBILITY

All pollen and macrofossil data are publicly available from the Neotoma Paleocology Database (<http://www.neotomadb.org/>).

BIOSKETCH

María Isabel Mujica is currently a Master’s student at the Facultad de Ciencias of the Universidad de Chile in Santiago, Chile, and a graduate student affiliate of the Institute of Ecology and Biodiversity (IEB). She is interested in past, present and future plant distribution patterns and is currently studying factors that control the distributions of Chilean orchids.

Author contributions: M.I.M. performed all plant macrofossil analyses and figures. M.I.M., C.L. and C.M.S. did most of the writing. A.M. and L.G-S performed all pollen analyses and together with C.L. contributed with writing and data analyses. R.P.H. contributed with geochronological analyses. R.P. contributed data on modern cacti populations, and helped in plant macrofossil identifications as well as in the writing. C.L., A.M. and C.M.S. designed the research and obtained the necessary funding.

Editor: Mark Bush