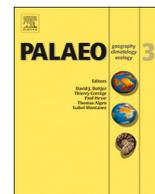




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Human resilience to Holocene climate changes inferred from rodent middens in drylands of northwestern Patagonia (Argentina)

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ABSTRACT

We reconstruct the Holocene vegetation, climate, and archaeological history for drylands of northwestern Patagonia, Argentina, based on multiproxy analysis (plant macrofossil, pollen, and parasites) of rodent middens integrated with a database of ¹⁴C dates associated with human occupations. The local scale corresponds to the Huenul paleoecological and archaeological locality, emplaced in north-western Patagonia (Neuquén Province, Argentina). The rodent midden record from the Huenul series reflects subtle vegetation changes driven by climatic variability at millennial timescale. Drier than present environmental conditions prevailed during the early Holocene (10,500–9400 cal yr BP), peaking during the mid-Holocene (9200–5500 cal yr BP), when wetter than present conditions established during the late Holocene (4400–2500 cal yr BP). These environmental and climatic dynamics agree with other paleoclimatic records from northern Patagonia, suggesting the winter precipitation dynamics related to the Southern Westerlies as a common driver. The diachronic distribution of anthropogenic radiocarbon dates from the western area of the South American Arid Diagonal between 32°–40°S conforms to a fitted exponential model of steady background population growth, not suggesting significant demographic changes that may have been the result of the impact of climate change. This record indicates that these human populations coped successfully with aridity, particularly during the mid-Holocene. These findings reinforce the need to integrate multi-scalar interdisciplinary analyses to assess the impact of climate change in human societies.

1. Introduction

The South American Arid Diagonal (SAAD) is a major climatic and biogeographic region, which is oriented NW-SE from Peru to southern Argentina, encompassing most of the arid and semiarid ecosystems of South America (Fig. 1; Gourou and Papy, 1966). The impact of dry periods on ancient human societies inhabiting these peri-Andean drylands is an important topic for archaeology, particularly during mid-Holocene times, when more arid conditions than present prevailed in the region (e.g., Núñez and Santoro, 1988; Gil et al., 2005; Garvey,

2008; Méndez et al., 2015; Barberena et al., 2017). However, the debate has been hampered by the lack of local paleoecological archives from the drylands themselves, imposing the need to compare against more distant archives, usually from lakes or peat bogs from humid settings near the Andes. In recent decades, rodent middens have provided important paleoclimatic proxy data directly from within the arid and semi-arid areas of the SAAD that contribute to this research topic (e.g. Betancourt et al., 2000; Maldonado et al., 2005; de Porras et al., 2017).

Fossil rodent middens are complex accumulations of local vegetation, nesting materials, insect remains, bones, sediment and feces,

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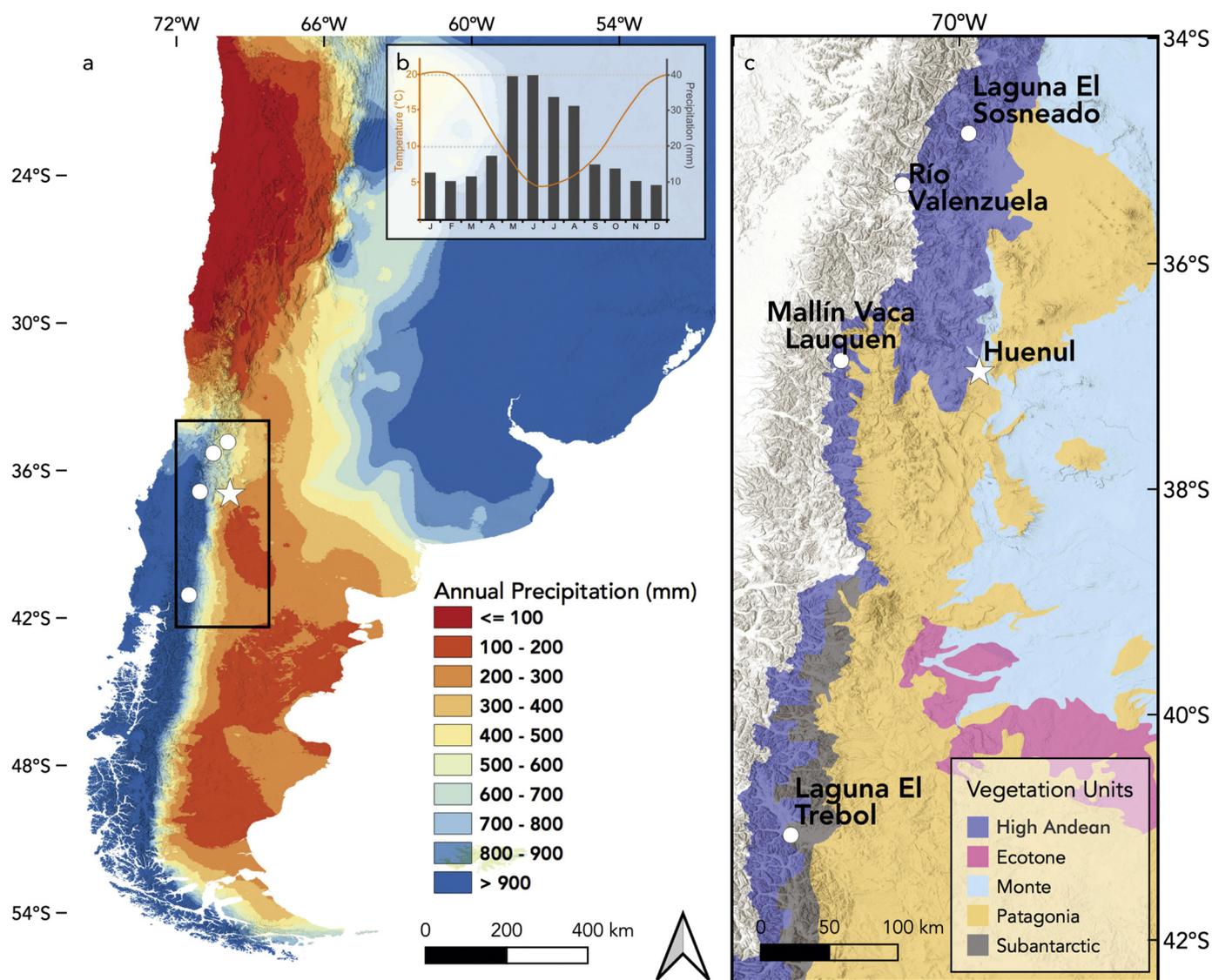


Fig. 1. (a) Annual precipitation map of southern South America (Fick and Hijmans, 2017) showing the South America Arid Diagonal (SAAD) as the area under 400 mm of annual precipitation, location of the study area and sites mentioned in the text; (b) climograph for Buta Ranquil, a town located 10 km southwards Huenul locality and; (c) regional vegetation map based on Oyarzabal et al. (2018) including sites mentioned in the text. Base map was plotted using QGIS 3.12. applying the ESRI World Hillshade.

preserved underneath rock slabs and within caves, that provide an excellent paleoecological archive of desert ecosystems (e.g., Betancourt et al., 1990, 2000; Latorre et al., 2003; Maldonado et al., 2005; Chase et al., 2013; de Porras et al., 2017). Previous evidence indicates that these deposits have been built in South America over the last 50,000 years or more, by four families of rodents (Abrocomidae, Chinchillidae, Muridae, and Octodontidae). While the widespread presence of these deposits across the SAAD is well-documented (Betancourt and Saavedra, 2002; see also Markgraf et al., 1997; Hofreiter et al., 2003), these fossil deposits have not been systematically studied eastwards of the Andes. Rodent middens provide fundamental archives in arid and semiarid areas of northwestern Patagonia, since standard sedimentary environments (lakes, fens) are usually temporary, and largely desiccated during the summer. Hence, there is a large and still unexploited analytical potential in these fossil deposits.

In this paper we present the results of an interdisciplinary project seeking to reconstruct changes in vegetation, climate, and human presence in drylands of northwestern Patagonia since the early Holocene times. We deploy a multi-scalar approach. First we present local scale

fossil rodent midden data (plant macrofossil, pollen, and paleoparasite records) from the Huenul study site in Neuquén Province, Argentina (36°57'S, 69°49'W; 1000 masl), located in the Monte drylands close to the ecotone with more humid Patagonian vegetation (Fig. 1). Second, we develop an interdisciplinary approach, combining fossil rodent midden data with a regional program of archaeological survey and excavation aimed to determine the timing and biogeographic pattern of human occupation of the northern Patagonian deserts (Barberena, 2015; Barberena et al., 2015a; Beltrame et al., 2016; Rughini et al., 2020). Significantly, the Huenul study site provides a sequence of fossil rodent middens associated to the archaeological archive of Cueva Huenul 1 site, which provides evidence of a discontinuous human occupation since the Pleistocene-Holocene transition (Barberena, 2015; Barberena et al., 2015b; Fernández et al., 2012). Thirdly, we move on to regional and macro-regional scale by integrating available paleoecological and archaeological evidence. The temporal fluctuations in human presence in the drylands are analyzed by using ^{14}C dates from archaeological contexts as a proxy of density of human occupation (Shennan et al., 2013; Williams et al., 2013; Timpson et al., 2020). On this basis, we reassess the previous suggestions about the impact of

climate change on human populations throughout the Holocene.

2. Ecological and paleoecological background

2.1. Modern setting

Northwestern semiarid Patagonia (36–37°S; 69–70°W; Neuquén province) lies on the eastern side of the Andes near the western limit of the SAAD at 36°S (Fig. 1a). The Andes function as a topographic barrier to the prevailing westerly storm tracks, affecting the patterns of atmospheric circulation and imposing a steep west-east gradient on precipitation and effective moisture (Garreaud et al., 2009). Annual precipitation varies from ca. 1100 mm close to the current Argentina-Chile border to 200–150 mm in the core of the SAAD at 36°S (Gourou and Papy, 1966; Fig. 1a). Most of the precipitation (~75%) falls during winter associated to moisture sourced from the Pacific Ocean brought by the Southern Westerlies system (Viale et al., 2019), while summer precipitation related to Atlantic moisture is negligible in this area (Fig. 1b).

Vegetation distribution follows this precipitation gradient, from forest communities west of the Andes (Chile) and confined to the Andean slopes in Argentina, giving way eastwards to the grass-steppes of the Patagonia Province, characterized by a low shrubby steppe intermingled with tussock grasses (Fig. 1c). The Poaceae family is prevalent in its floristic composition and the genus *Stipa* is dominant. Other significant components of the grass flora are *Poa*, *Festuca*, and *Bromus*. Shrubs with cushion-like appearance physiognomically characterize large areas. The most frequent shrub species are *Chuquiraga* spp., *Colliguaja intergerrima*, *Azorella prolifera*, *Senecio filaginoides*, *Berberis heterophylla*, *Baccharis darwinii*, *Anarthrophyllum rigidum*, *Nassauvia glomerulosa*, *Lycium chilense* and *Trevoa patagonica* (Chiappella and Ezcurra, 1999; León et al., 1998). As altitude and precipitation decrease towards the eastern Argentinean lowlands, the ecotone with the shrub-steppes of the Monte Province that characterize drylands at this latitude develop (Fig. 1c). The Monte province comprises a xeric 0.5–1.5 m-tall shrubland dominated by *Larrea* spp. associated with shrubs like *Lycium*, *Chuquiraga*, *Prosopis*, *Ephedra*, *Gutierrezia*, *Verbena*, *Baccharis*, *Bougainvillea spinosa* and *Schinus polygamus*, dwarf shrubs (e.g. *Accanthisiphia seriphoides*, *Perezia recurvata*), herbs (e.g. *Hoffmanseggia* spp., *Plantago patagonica*), and grasses (e.g. *Stipa* spp., *Poa ligularis*) (León et al., 1998). The Monte-Patagonia transition is characterized by a 1.5 m shrubland dominated by Monte elements such as *Prosopis denudans*, *Schinus polygamus*, *Larrea nitida*, *Posopidastrum globosum* and *Verbena* sp., along with dwarf shrubs such as *Mulinum spinosum*, *Senecio filaginoides*, *Grindelia chilensis*, *Nassauvia glomerulosa*, *Tetraglochin ameghinoi* and *Chuquiraga avellanadae* (Oyarzábal et al., 2018; Fig. 1c).

2.2. Paleoclimatic background

The environmental dynamics in northwestern Patagonia at the millennial/centennial scale are largely related to the frequency and intensity of frontal systems of the Southern Westerlies that bring precipitation to this region (Garreaud et al., 2009). However, the paleoenvironmental scenarios of northwestern Patagonia after the Last Glacial Maximum are far from clear given the scarcity of records, which are low resolution and highly discontinuous through time. Indeed, there is almost no local information about the past environments at northwestern Patagonia (36°S) inhabited by the extinct mega-mammals and later by the early hunter-gatherer human groups colonizing northern Patagonia.

Even though the SAAD has remained relatively stable since its origin during the Pliocene (Villagrán and Varela, 1990), global and regional climate change during the late Quaternary has produced important changes in the distribution of plants, animals, and human populations (Betancourt et al., 2000; Grosjean et al., 2003; Latorre et al., 2013; Méndez et al., 2015; Barberena et al., 2017). Thus, available knowledge

on the paleoclimatic and paleoenvironmental dynamics of this region is largely based on only three archives (Fig. 1a): (1) pollen and charcoal records from Mallín Vaca Lauquen (MVL) (36°51'S; Markgraf, 1987; Markgraf et al., 2008), (2) glacial fluctuations from Río Valenzuela (RV) (35°S; Espizúa, 2005; Espizúa and Pitte, 2009), and (3) pollen and charcoal records from Laguna El Sosneado (LES) (35°S; Navarro et al., 2012).

During the late Glacial (17,500–14,800 cal yr BP), MVL suggests that conditions were colder and drier than present, associated with a reinforcement of the southeastern Pacific Anticyclone, which blocked the incursion of frontal systems into northern Patagonia (Markgraf et al., 2008). Since 14,800 cal yr BP, and up to the early Holocene (8000 cal yr BP), the conditions became wetter and warmer than before (while still colder and drier than present conditions). Since then, more variable precipitation conditions along with increased temperature values occurred in the MVL area up to 5300 cal yr BP (Markgraf et al., 2008). However, the pollen and charcoal records of LES identified conditions more humid than present 6400–5000 cal yr BP (Navarro et al., 2012), which are synchronous with three glacial advances recorded in the RV basin dated between 6400 and 4800 cal yr BP. This suggests a precipitation increase in the Andean highlands (Espizúa, 2005; Espizúa and Pitte, 2009). During the last 5000 cal yr, MVL shows the establishment of similar conditions than present but under a high variability (Markgraf et al., 2008), whereas RV glaciers show an advance at 2600–2500 cal yr BP synchronous with a wet phase recorded in LES (3200–2000 cal yr BP). Finally, RV glaciers show a final advance at 600 cal yr BP that can be associated with the Little Ice Age (Espizúa, 2005; Espizúa and Pitte, 2009), which is followed by the onset of a dry phase (LES) at 500 cal yr BP (Navarro et al., 2012).

3. Materials and methods

3.1. Sampling of the rodent middens

A fossil series of 16 rodent middens from Huenul locality (Neuquén province, Argentina; 36°57'S; 69°49'W; 1000–1050 masl; Figs. 1c, 2a) was collected. The middens were extracted by using a hammer and chisel, cleaned in the field for weathering rinds and surface contaminants, and split along clear stratigraphic units where recognizable. Each midden was separated in the laboratory into subsamples to perform the plant macrofossil and pollen analysis (Fig. 2b). Fecal pellets were taken from the plant macrofossil subsample from each midden for parasite analysis and for radiocarbon dating by AMS and conventional methods (see details below).

3.2. Radiocarbon dating of the middens and phase model comparison with human occupations

The age of each midden was obtained through ¹⁴C AMS or conventional radiocarbon dates performed on 3 to 10 g of fecal pellets. The radiocarbon dates were calibrated to calendar years BP using the SHCal13 calibration curve for the Southern Hemisphere (Hogg et al., 2013) using bespoke scripts in R (R Core Team, 2014).

To test if rodent and human occupations in the Huenul area (local scale) were concurrent or mutually exclusive, we innovate a formal model comparison approach. The null hypothesis (model 0) defines a concurrent presence of humans and rodents and therefore assumes all 32 ¹⁴C dates (16 anthropogenic and 16 from rodent middens) are random samples from a single continuous phase between 12,000 and 300 cal yr BP. Model 1 introduces a single parameter (the date of a phase boundary) which separates this time span into two phases, an exclusively human phase followed by an exclusively rodent phase (human – rodent). Model 2 comprises two date parameters to create three mutually exclusive phases (human – rodent – human). We continue in this way up to and including model 7, with each subsequent model potentially fitting closer to the data but requiring a greater

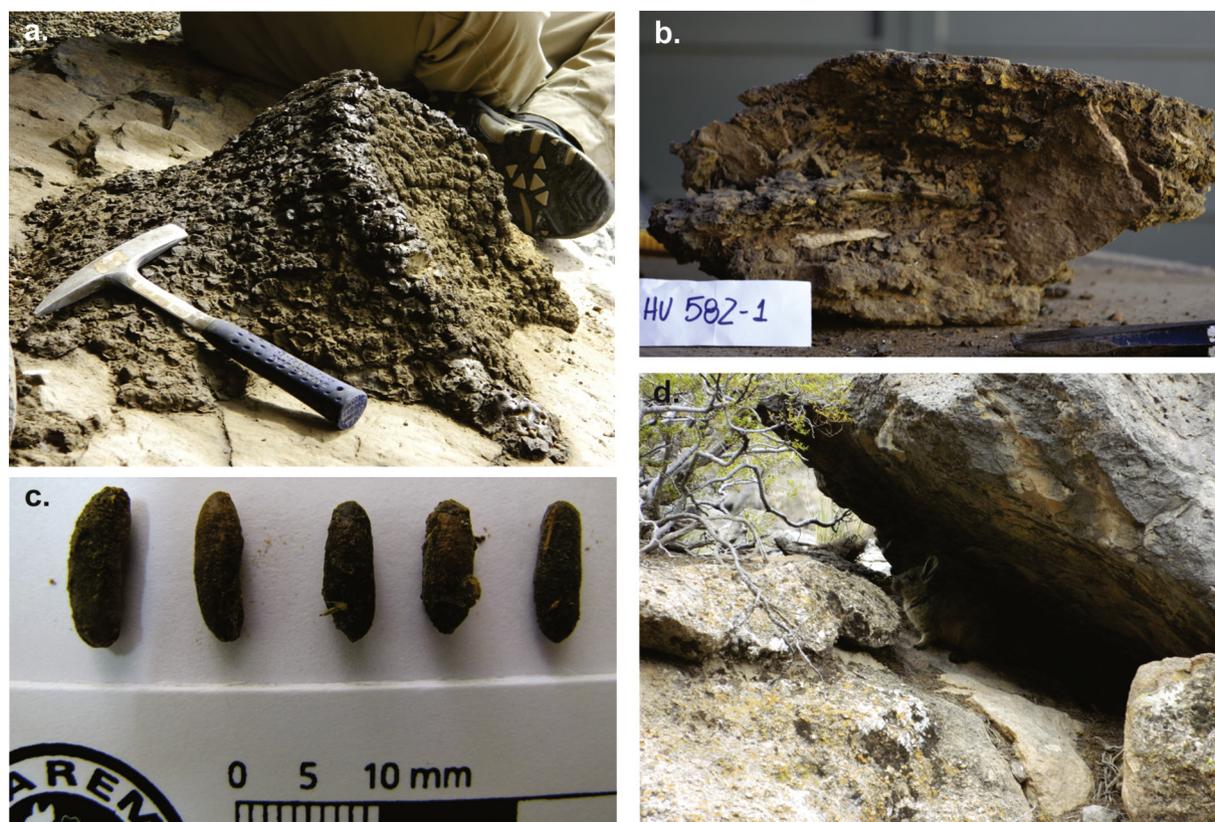


Fig. 2. Photographs showing (a) midden found underneath an ignimbrite; (b) rodent midden HU582-1 while being subsampled in the laboratory; (c) fecal pellets under characterization; (d) a vizcacha (*Lagidium viscacia*) observed around Huenul locality, a potential builder of the middens.

number of parameters to achieve this. We assess the balance between this goodness of fit and model complexity using the Bayesian Information Criterion (BIC) (Schwarz, 1978). Further methodological detail is provided in the Supplementary Material S1.

3.3. Analysis of paleoparasites, macro-botanical remains and pollen

The paleoparasitological study performed on rodent fecal pellets included samples of the 16 rodent middens, ten of which have been previously analyzed (Beltrame et al., 2016). Five fecal pellets from each midden were externally examined, fully processed, rehydrated in a 0.5% water solution of tri-sodium phosphate, homogenized, subjected to spontaneous sedimentation and examined through light microscopy (Beltrame et al., 2016).

The plant macrofossil subsamples were soaked in 10 L buckets of water for two to three weeks to dissolve urine (amberat), wet-sieved through a 0.825 mm mesh and placed in a drying oven at 50–60 °C for three days. Macrofossils (plants, vertebrate bone, rodent fecal pellets and insects) were separated according to standard techniques (Betancourt et al., 1990; Latorre et al., 2002). Plant macrofossils were identified to the highest possible taxonomic level through a qualitative and quantitative analysis of diagnostic macroscopic characters which were compared with the extensive reference collection of modern flora hosted at the Facultad de Ciencias Aplicadas a la Industria (FCAI, Universidad Nacional de Cuyo) and published references (Esau, 1960; Martin and Barkley, 1973; Palacios and Bravo, 1974–1975). The analysis of plant macrofossils was carried out under a stereomicroscope (Nikon SMZ800) at 1–8× magnification. Main qualitative characters included shape and color of seeds and leaf limbs, patterns of main nerves, leaf margin characteristics, ornamentation of the seminal cover, state of preservation (e.g. complete, broken). Quantitative characters consist of (leaf, seeds, fruits, etc.) maximum length and maximum width, seed maximum diameter of the fissure line and opening of the

fissure line between its free ends, fruit maximum thickness of the epicarp, mesocarp and endocarp. As quantitative methods, such as absolute counts or pooled weights of individual species, are time consuming and ultimately biased by midden size and dietary preferences, each taxon was quantified by using a Relative Abundance Index (RAI) where 0 = absent, 1 = rare, 2 = common, and 3 = dominant (Spaulding et al., 1990). The RAI is a quick method for estimating past variations in vegetation composition (Spaulding et al., 1990). Plant species nomenclature follows the published 'Catálogo de las Plantas Vasculares del Conosur' (<http://www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm>). The taxa found were assigned to biogeographic units, except for *Maihuegniopsis*, given its wide distribution encompassing more than one biogeographic unit (Kiesling, 1984) and *Atriplex*, considered as azonal vegetation related to saline soils mostly related to desiccation in the study area (Passera and Borsetto, 1989).

The pollen analysis subsamples were hydrated 24–48 h and sieved through a 120 µm mesh to separate macro- (plant, seeds, feces, etc.) and micro-remains (midden matrix), and a 1 cm³ aliquot of the micro-remains from each midden was processed following standard methods for pollen extraction (Faegri and Iversen, 1989). At least 300 pollen grains were counted for each sample which were identified based on the reference collection of Laboratorio de Paleoecología y Paleoclima (CEAZA) and published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978). Amaranthaceae and *Nothofagus* (*dombeyi* type) were excluded from the basic pollen sum, given that the first one corresponds to azonal vegetation growing within a perennial stream close to the Huenul locality and the second one is a long-distance pollen type produced by sub-Antarctic forests located westwards in the Andes. A Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 1987) was performed to divide the fossil midden sequences into zones, considering all pollen taxa included into the basic sum and contributing > 2%.

Pollen percentages, CONISS cluster analysis and pollen and plant

macrofossil diagrams were calculated and plotted, respectively, using TGView 1.7.16 (Grimm, 2011).

The interpretation of the pollen and macro-botanical remains records was carried out considering that the Huenul locality is currently located at the Monte-Patagonia transition (Fig. 1c). According to the regional relationships between precipitation and vegetation gradients (see Modern Setting section), an increase in pollen percentages or RAI values of Monte taxa (Patagonian taxa) would mean a decrease (increase) of moisture. Therefore, a qualitative artificial moisture scale was created: D (drier than present), D⁺ (slightly drier than present), W (slightly wetter than present) and W⁺ (much wetter than present).

3.4. Temporal fluctuations in human populations

We assemble a database comprising 580 radiocarbon dates from 244 archaeological sites from the central-western part of the SAAD (32°–40°S, Mendoza and Neuquén provinces; Argentina) by merging and updating previous compilations (Supplementary Material S2; Barberena et al., 2015a; Gil et al., 2014; Gordón et al., 2019). On this basis, we reconstruct human population fluctuations through time using a Summed Probability Distribution (SPD), and test for significant fluctuations from a null exponential distribution following an established approach which compares the observed SPD with simulated SPDs generated under a null model of long-term exponential demographic growth and taphonomic loss (Shennan et al., 2013). This approach can identify unusual fluctuations through time that significantly depart from the null model, from which past demographic events can be inferred. Further methodological detail is provided in Supplementary Material S1.

4. Results

4.1. Radiocarbon dating and modeling rodent and human occupation phases at Huenul Locality

The sequence of radiocarbon dates at Huenul is composed of 32 samples across a 12,000-year period (Table 1): 16 samples are anthropogenic dates from the site Cueva Huenul 1 located in the same rocky outcrop (Barberena, 2015) where the middens were collected, and the remaining 16 samples were obtained from the rodent middens. Fig. 3 juxtaposes the summed probability distributions of these dates classes. The blocks of pale red and blue show the five modeled phases of alternating human – rodent occupation, under the best model. The maximum likelihood parameter estimates for the phase transition dates in model 4 (Table 2) suggest three human occupancy phases at Huenul: firstly, between 12,000 and 10,339 cal yr BP (archaeological component 1), secondly a very short phase between 5553 and 5472 cal yr BP (component 3), and thirdly a phase between 1704 and 300 cal yr BP (component 4). Additionally, we have also recorded a paleontological component 1 dated to the late Pleistocene (16,695 to 13,631 cal yr BP), for which no human occupations were recorded (see detailed contextual information in Barberena, 2015; Barberena et al., 2015b).

When comparing the dates for rodent middens and human occupations, our results show that model 4 best fits the data (lowest BIC, Table 2), and the Bayes Factor shows this is over 9 million times more likely than model 0, allowing us to reject the hypothesis that humans and rodents coexisted throughout the 12,000-year period, and instead favoring the most likely model that their respective occupancies were mutually exclusive in alternating discrete phases. This finding indicates a lack of occupational superimposition on the local scale of the rocky outcrop of the Huenul locality, not necessarily implying that this is a regional pattern. Indeed, *Lagidium* is represented in the zooarchaeological record of Cueva Huenul 1, suggesting that humans occasionally hunted and consumed them (Fernández et al., 2012). Models 1, 2 and 3, on the other hand, perform badly and are substantially poorer than the null hypothesis. From model 4 onwards, the maximum likelihood is

higher than for the null model and continues to improve with each additional parameter. However, the lack of improvement in the BIC after model 4 shows that this increasing complexity is not justified and results in over fitting.

4.2. Agents of midden-formation: a paleoparasitological assessment

A total of 21 of the 60 fecal samples contained parasites. The eggs of parasites found were assigned to *Heteroxyrema* (Cavioxyura) viscaciae Sutton and Hugot, 1989 and *Helminthoxys* sp. (Nematoda: Oxyuridae), *Trichuris* sp. (Nematoda: Trichuridae), and one unidentified nematode. Based on the rodent species present in the study area (Fernández et al., 2015; Pardiñas and D'Elía, 2015), the aspect of fossil rodent middens and of the coprolites examined (Fig. 2c), the eggs of the parasites found, and the knowledge of the parasitic fauna of vizcachas, the feces were attributed to the mountain vizcacha *Lagidium viscacia* (Caviomorph: Chinchillidae; Fig. 2d). Mountain vizcachas are large caviomorph rodents that inhabit arid regions of western and southern South America, from the highlands of Ecuador through the Andes of Peru and Bolivia to the coastal mountains of Chile and Patagonian steppe of Argentina. This rodent is found in rocky outcrops and is highly gregarious, living in colonies that may range widely in size (Spotorno and Patton, 2015). It is represented in low frequencies in the stratigraphy of Cueva Huenul 1 (Fernández et al., 2012). The biological cycle of parasites found were discussed in detail in Beltrame et al. (2016).

4.3. Plant macrofossil record

A total of 30 plant macrofossil taxa were identified for all samples, 13 of which were identified to the species taxonomic level and 17 to genus level (Fig. 4, Fig. 5; Table 3).

For samples with ages between 10,400–9400 cal yr BP, a total of 23 taxa were recorded. These samples are dominated (Relative Abundance Index: 3 = dominant) by Monte taxa such as *Prosopis* sp. associated with *Acantholippia seriphioides* and elements of Patagonia (*Baccharis* sp., *Adesmia* sp., *Berberis* spp., *Junellia seriphioides*, *Balbisia gracilis*, *Lupinus* aff. *oreophilus*, *Nassauvia axillaris*). Taxa such as *Schinus* sp. and *Ephedra* sp., characteristic of the Monte-Patagonia transition, are rare (RAI: 1 = rare), while the presence of cacti (*Maihuenia patagonica*) are recorded as frequent (RAI: 2 = common). Among the grasses, *Poa* sp. and *Hordeum* sp. are dominant (RAI = 3) while *Festuca* sp., *Bromus* sp. and *Jarava* sp. rare (RAI = 1).

For samples with ages of 9200, 6500 and 5700–5500 cal yr BP, the richness and diversity of species is the lowest for the whole record. Assemblages of plant macrofossils are dominated Monte taxa (RAI = 2 or 3) represented by *Prosopis* spp., *Larrea* sp., *Acantholippia seriphioides* except for the 5700 cal yr BP assemblage, which presents low abundance of Patagonia elements (*Baccharis*, *Junellia seriphioides*, and *Hordeum*). Those assemblages dominated by Monte taxa are associated to Monte-Patagonia transition taxa including *Schinus* sp., *Ephedra* sp. and *Hoffmannseggia* sp. which are rare (RAI = 1) while Patagonian taxa (RAI = 1 or 2) includes shrubs (*Baccharis* sp., *Adesmia* cf. *officinalis*, *Lupinus* aff. *Oreophilus*), dwarf shrubs (*Euphorbia* sp., *Perezia* aff. *recurvata* and *Nassauvia axillaris*), and grasses (*Festuca* sp., *Jarava* sp., and *Poa* sp.). are present. The cacti *Maihuenia patagonica* is also present at 6500 cal yr BP.

Prosopis sp. dominates (RAI = 2 or 3) along with other Monte taxa such as *Larrea* sp. and *Acantholippia seriphioides* (RAI = 1) between 4200 and 3800 cal yr BP in association with Monte-Patagonia elements including *Schinus* sp., *Ephedra* sp., and *Senecio* sp., as well as Patagonian elements (*Berberis* spp., *Junellia seriphioides*, *Gilia crassifolia*, *Mulinum spinosum*, *Nassauvia axillaris*, among others).

For samples with ages between 3500 and 2500 cal yr BP, the macrofossil assemblages are co-dominated by Monte elements (*Prosopis* sp. RAI: 3 = dominant), Monte-Patagonia transition elements such as *Schinus* sp. and *Ephedra* sp. (RAI < 2) and Patagonian (RAI < 2)

Table 1
Radiocarbon dates of Cueva Huenul 1 archaeological site and rodent middens from Huenul locality.

	Sample code	Material dated	Laboratory code	¹⁴ C Age	St. Dev.	δ ¹³ C (‰)	Calibrated age BP (median)	Source	
Cueva Huenul 1 – archaeological site	CH1.6	<i>Lama guanicoe</i> (bone)	AA-99102	373	43	−20.4	396	Barberena, 2015	
	CH1.4	Grass	AA-85721	1416	37	−23.0	1291	Barberena, 2015	
	CH1.7	<i>Lama guanicoe</i> (bone)	AA-99103	1590	46	−19.9	1440	Barberena, 2015	
	CH1.16	<i>Senna aphylla</i> (twigs)	AA-102575	4786	46	−25.0	5487	Barberena, 2015	
	CH1.8	<i>Lama guanicoe</i> (bone)	AA-99104	9375	91	−18.1	10,535	Barberena, 2015	
	CH1.9	<i>Lama guanicoe</i> (bone)	AA-99105	9295	90	−17.7	10,432	Barberena, 2015	
	CH1.15	<i>Prosopis</i> sp. (seed)	AA-102574	9402	60	−23.1	10,578	Barberena, 2015	
	CH1.1	Charcoal (hearth #2)	AA-85718	9531	39	−22.7	10,750	Barberena, 2015	
	CH1.10	<i>Lama guanicoe</i> (bone)	AA-99106	10,155	98	−20.6	11,694	Barberena, 2015	
	CH1.11	<i>Retanilla patagonica</i> (fruit)	AA-99100	9261	66	−19.8	10,388	Barberena, 2015	
	CH1.12	<i>Lama guanicoe</i> (bone)	AA-99109	1269	46	−20.2	1143	Barberena, 2015	
	CH1.14	<i>Lagenaria</i> sp. (gourd)	AA-102573	541	42	−26.8	526	Barberena, 2015	
	CH1.13	<i>Lama guanicoe</i> (bone)	AA-99110	1753	47	−20.2	1628	Barberena, 2015	
	CH1.17	<i>Lama guanicoe</i> (bone)	D-AMS 018771	1462	33	–	1320	Romero V. and Barberena, 2017	
	CH1.22	Macro-botanical remain charcoal	D-AMS 033195	983	29	−17.9	855	Llano, 2017	
	Huenul site – rodent middens	CH3.1	charcoal	AA-102576	1562	40	−22.1	1403	Fernández et al., 2017
		HU559A	Fecal pellets	LP- 3104	2540	80	−25 ± 2	2569	Beltrame et al., 2016
HU584A		Fecal pellets	LP-3094	3320	90	−25 ± 2	3512	Beltrame et al., 2016	
HU583–2		Fecal pellets	D-AMS 15904	3620	28	−21.7	3880	This paper	
HU558B		Fecal pellets	D-AMS 15897	3819	30	−23.2	4149	This paper	
HU559B		Fecal pellets	D-AMS 15902	3862	27	−14.9	4212	This paper	
HU583–1		Fecal pellets	D-AMS 15899	4058	29	−17.9	4483	This paper	
HU584B		Fecal pellets	D-AMS 15900	4765	25	−24.8	5466	Beltrame et al., 2016	
HU560		Fecal pellets	D-AMS 15898	4969	28	−18.8	5647	This paper	
HU558D		Fecal pellets	LP- 3108	5730	70	−25 ± 2	6480	Beltrame et al., 2016	
HU582–1		Fecal pellets	LP- 3102	8280	120	−25 ± 2	9213	Beltrame et al., 2016	
HU559DB		Fecal pellets	D-AMS 15903	8433	39	−20.7	9426	This paper	
HU558E1		Fecal pellets	D-AMS 15901	8438	37	−18	9433	Beltrame et al., 2016	
HU558C		Fecal pellets	LP- 3100	8680	120	−25 ± 2	9963	Beltrame et al., 2016	
HU558E2		Fecal pellets	LP- 3098	8830	90	−25 ± 2	9834	Beltrame et al., 2016	
HU558A2		Fecal pellets	LP- 3112	8920	180	−25 ± 2	9947	Beltrame et al., 2016	
HU558A1		Fecal pellets	LP- 3115	9240	130	−25 ± 2	10,389	Beltrame et al., 2016	

including shrubs such as *Berberis* spp., *Junellia seriphoides*, *Mulinum spinosum*, *Nassauvia axilaris* and grasses (*Festuca* sp., *Jarava* sp. and *Poa* sp.).

4.4. Pollen record

The pollen record of the Huenul rodent midden series comprises a total of 30 pollen types (Fig. 6) and is divided in two zones and two subzones (Fig. 7):

Zone HU1a (10,400–9400 cal yr BP) is dominated by *Larrea*

(50–15%) associated with *Prosopis* (25–5%), Solanaceae (*Lycium* type; 10%), *Schinus* (20–5%), *Ephedra* (25–5%) and Poaceae (15–5%). Ast subf Ast (*Senecio* type), Fabaceae (*Adesmia* type), Ast subf Ast (*Baccharis* type) and Ast subf Mut (*Chuquiraga*) are present in percentages under 12%. Amaranthaceae, an azonal pollen type (and therefore excluded from the basic pollen sum) growing in the perennial stream in Huenul locality.

Zone HU1b (9200, 6500 and 5700–5500 cal yr BP) is dominated by *Larrea* (60–25%) along with *Prosopis* (< 20%), Solanaceae (*Lycium* type; < 20%), *Schinus* (< 10%) and Poaceae (20–5%). Other Monte or

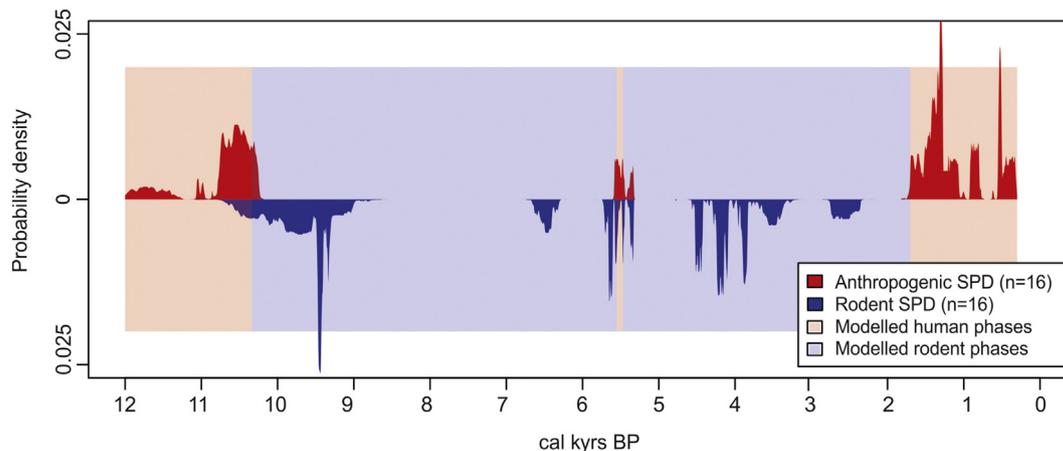


Fig. 3. Summed Probability Distributions (SPD) of calibrated radiocarbon dates from human occupations (red) at Cueva Huenul 1 and rodent middens (blue) from Huenul locality. Note that the rodent middens SPD y-axis is inverted to aid the comparison with human occupations SPD. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

Summary of the seven models utilized in the phase model comparison of the timing of human occupations and rodent middens in the Huenul Locality. Model 4 (phases of human – rodent – human – rodent – human occupancy) has the lowest value for the Bayesian Information Criterion -BIC, indicated in bold-(parameter date estimates are aligned to show similarities between models).

Model	Maximum likelihood parameter estimates (yr BP)	Log likelihood	Bayesian information criterion
0		-299.75	599.51
1	9350	-3143.70	6290.88
2	10,307, 3290	-434.91	876.76
3	10,308, 3290, 303	-434.91	880.22
4	10,339, 5553, 5472, 1704	-276.79	567.45
5	10,339, 5553, 5472, 1704, 315	-276.77	570.87
6	1780, 10,767, 10,368, 5550, 5474, 1698	-273.88	568.55
7	11,783, 10,766, 10,369, 5550, 5474, 1698, 326	-273.80	571.86

Patagonia pollen types are present in percentages under 10%, whereas Amaranthaceae values ranges between 35 and 20%.

Zone HU2a (4200–3800 cal yr BP) is co-dominated by *Larrea* (< 20%), *Ephedra* (40–10%), Ast subf Ast (*Senecio* type), Poaceae (25–20%) along with *Schinus*, Ast subf Ast (*Baccharis* type), Fabaceae (*Adesmia* type), Ast subf Mut (*Chuquiraga* and *Proustia*, *Nassauvia* types) and Apiaceae (*Mulinum* type) with values under 15%. Amaranthaceae

values remains under 25%.

Zone HU2b (3500 and 2500 cal yr BP) is a subzone integrated by two pollen assemblages quite different to each other. The older one dominated by *Larrea* (45%) along with Solanaceae (*Lycium* type; 15%) and Poaceae, whereas the younger one is co-dominated by *Larrea* (10%), *Ephedra* (20%), Ast subf Ast (*Senecio* type; 15%) and Poaceae (20%). Amaranthaceae values are under 20%.

4.5. Summed probability distribution analysis of the ^{14}C database

The overall anthropogenic database comprises 580 ^{14}C dates from 244 sites. We constrain our study period to 12,000 to 500 cal yr BP, which encompasses 573 calibrated dates from 240 sites. Fig. 8 shows the Summed Probability Distribution (SPD) of this database, which conforms extremely well to a fitted exponential model of steady background population growth and taphonomic loss. Although there are a few sections of the SPD that sit outside the null 95% CI ribbon, these are few, sporadic, and the size of their deviation is only marginally outside the ribbon. As such, these are to be expected given that approximately 5% of any random simulation can be expected to sit outside the ribbon, and therefore can be considered false positives. Indeed, the p-value of 0.4265 means that we cannot reject the null hypothesis.

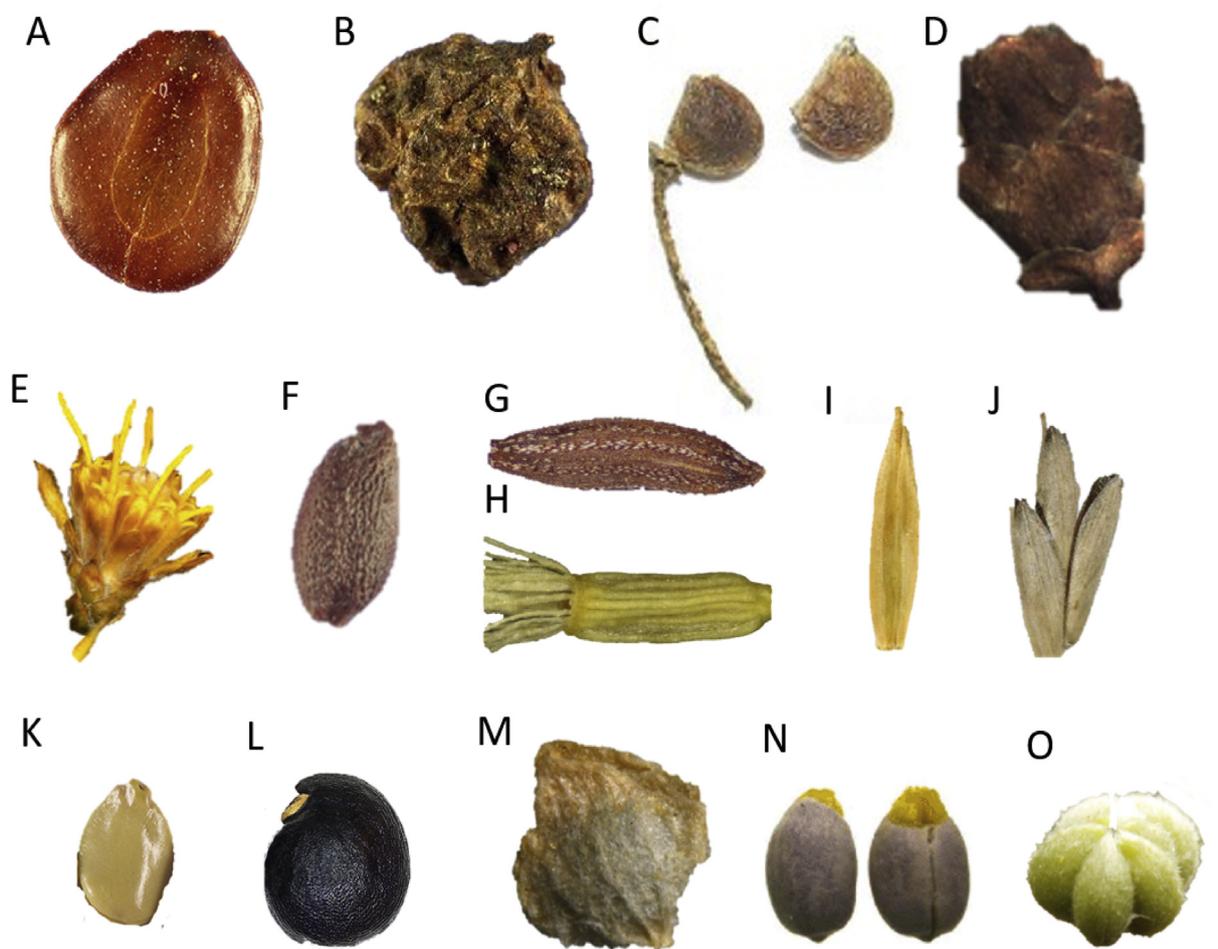


Fig. 4. Photographs of plant macrofossil found in the Huenul rodent middens (A) *Prosopis* sp. seed, (B) *Schinus* sp. fruit, (C) *Adesmia* aff. *corymbosa* fruit, (D) a seed *Ephedra* sp. inside the strobilus, (E) *Chuquiraga oppositifolia* flower receptacle; (F) *Berberis* sp. seed; (G) *Senecio* sp. cypsela, (H) *Baccharis* sp. cypsela, (I) *Festuca* sp. fruit, (J) *Bromus* sp. spikelet, (K) *Hoffmannseggia* sp. seed, (L) *Maihuenia patagonica* seed, (M) *Atriplex* sp. bracteole, (N) *Euphorbia* sp. seed, (O) *Larrea* sp. fruit.

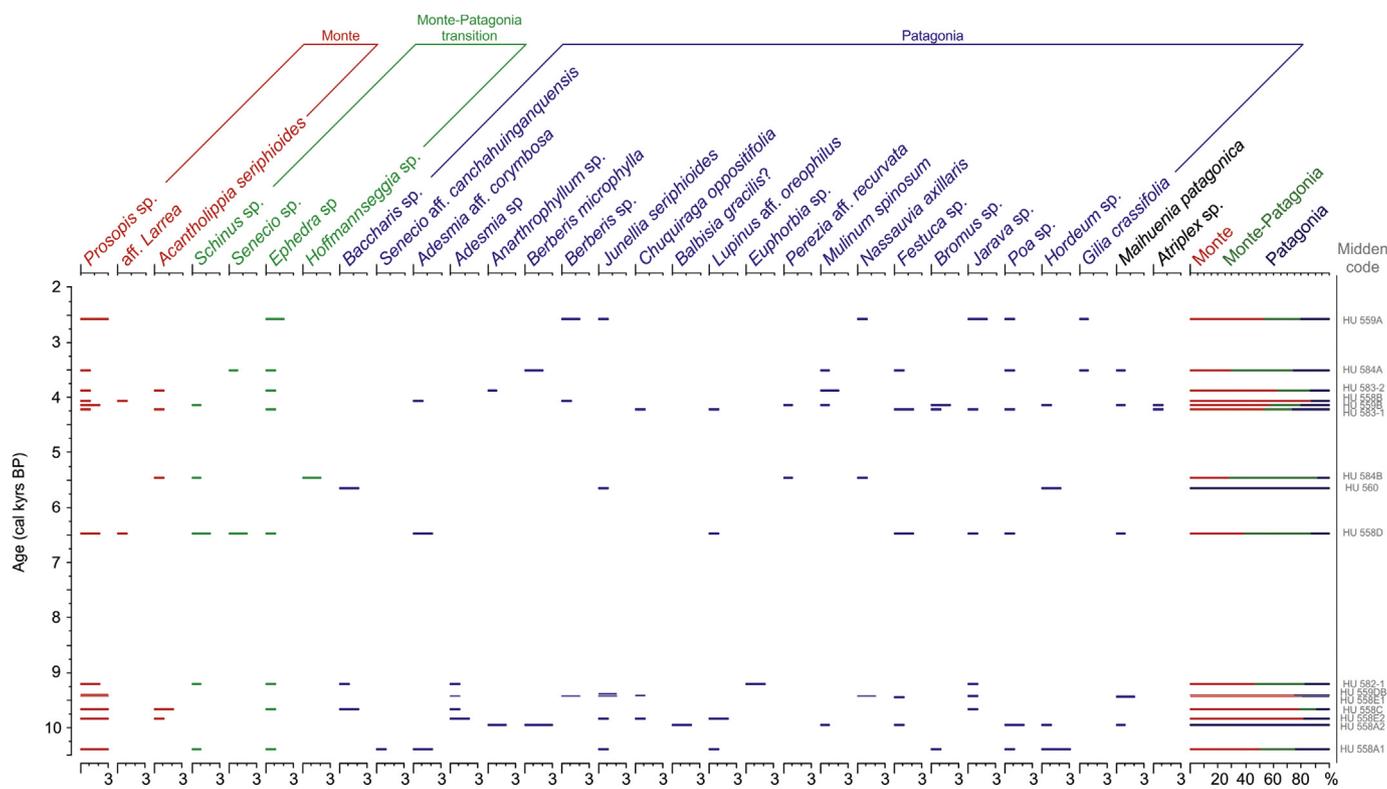


Fig. 5. Diagram of plant macrofossil of Huenul rodent midden series showing the Relative Abundance Index (RAI) and the integrated percentage diagram of RAI according to the biogeographic affinity of macrofossils. RAI values mean 0 = absent, 1 = rare, 2 = common, and 3 = dominant.

5. Discussion

5.1. *Lagidium* as a midden-forming agent

On the basis of the aspect of fossil rodent middens, the characteristics of the coprolites examined, the knowledge on the parasitic fauna of vizcachas, and the eggs of the parasites found (*Heteroxyrema* [Cavioxyura] *viscaciae* and *Helminthoxys* sp. [Nematoda: Oxyuridae]), the feces were attributed to the mountain vizcacha *Lagidium viscacia* (locally known as chinchillón or vizcacha), which we assigned as the only producer of the Huenul series midden record. Indeed, *Lagidium* is one of the main midden-producers throughout semi-arid and arid South America (Betancourt and Saavedra, 2002). It is a syntopic rodent of medium size (ca. 2000 g) that belongs to the Chinchillidae family (Redford and Eisenberg, 1992). In Argentina it inhabits exclusively rocky environments with scarce vegetation cover, either in the high peaks of the Andes even above 3000 masl, or in the isolated canyons and fences of extra-Andean Patagonia. The vizcachas are an herbivore-rodents with morning and crepuscular habits and a foraging range that is concentrated within 30 m from the rocky outcrops that it occupies, where they live in family groups (Walker et al., 2000). The restricted foraging activity of the vizcacha suggests that the macrofossil botanical record from the middens is a proxy of the vegetation cover in the immediate surroundings of the middens. In terms of diet, the vizcacha has a specialized feeding behavior despite its consumption of a wide variety of plant species (Galende et al., 1998; Galende and Raffaele, 2012). However, this feeding behavior was particularly observed in grass-dominated environments, while no similar surveys are available for vizcachas living into shrub dominated landscapes like the Monte around Huenul locality.

5.2. Pollen vs. plant macrofossils record

The pollen and plant macrofossil records show similar

environmental changes in time and direction, but there are differences related to the spatial scales represented by these proxies and by their taphonomy. Thus, the pollen record reflects changes of greater magnitude than the macrofossil record. However, changes in abundance and diversity in the macrofossil record complement at a local scale the regional trends of vegetation changes informed by the pollen record.

While pollen of azonal (Amaranthaceae) and long distance plants (*Nothofagus*) are present in the midden pollen assemblages, they are poorly represented or completely absent in the macrofossil record, respectively, due to the pollination syndrome of species within those family/genera and the different spatial scales represented by the pollen (local/regional) and plant macrofossil (local) records. On the other hand, plant macrofossil assemblages show a clear decrease in diversity during the mid-Holocene that is not reflected as clearly in the pollen record, which only shows a decrease in pollen percentages of many Monte-Patagonia transition and Patagonia pollen types. Similar issues were described and discussed earlier regarding pollen and macrofossil records preserved in rodent middens from the Atacama Desert, located northwards in the SAAD (Maldonado et al., 2005; de Porras et al., 2017).

5.3. Environmental reconstruction

Plant macrofossil and pollen records from the Huenul midden series synchronously reflect the occurrence of moderate environmental and vegetation changes in the Monte-Patagonia ecotone at 36°S since the early Holocene (Figs. 5, 7).

During the early Holocene (10,500–9400 cal yr BP), Monte-like vegetation dominated by tall shrubs such as *Prosopis*, *Larrea* and *Lycium*, along with Monte-Patagonia transition elements (e.g. *Schinus*, *Ephedra*), occurred around Huenul indicating dry conditions (even drier than present ones) at the local and regional scales. The high percentages of Amaranthaceae, azonal plants growing into the ephemeral streams, indicate however, alternating dry and wet phases which may reveal a

Table 3

List of plant species identified in the rodent midden macrofossil record of Huenul locality.

Taxa	Family	Phytogeographical affinity	Identified plant part
Gymnospermae			
<i>Ephedras</i> pp.	Ephedraceae	Monte-Patagonia transition	Seed, bark
Angiospermae			
<i>Baccharis</i> sp.	Asteraceae	Patagonia	Leaves
<i>Chuquiraga oppositifolia</i>	Asteraceae	Patagonia	Leaves, bluegrass
<i>Nassauvia axillaris</i>	Asteraceae	Patagonia	Leaves
<i>Perezia aff. recurvata</i>	Asteraceae	Patagonia	Leaves
<i>Senecio</i> aff. <i>canchahuinganquensis</i>	Asteraceae	Patagonia	Leaves
<i>Senecio</i> sp.	Asteraceae	Monte-Patagonia transition	Leaves
<i>Schinus</i> sp.	Anacardiaceae	Monte-Patagonia transition	Endocarp
<i>Mulinum spinosum</i>	Apiaceae	Patagonia	Stem
<i>Berberis</i> sp.	Berberidaceae	Patagonia	Seed, bark
<i>Berberis microphylla</i>	Berberidaceae	Patagonia	Leaves, seed
<i>Maihueia patagonica</i>	Cactaceae	wide distribution	Seed
<i>Atriplex</i> sp.	Chenopodiaceae	azonal	Bract
<i>Euphorbia</i> sp.	Euphorbiaceae	Patagonia	Seed
<i>Adesmia</i> aff. <i>corymbosa</i>	Fabaceae	Patagonia	Leaves
<i>Adesmia</i> sp.	Fabaceae	Patagonia	Leaves
<i>Anarthrophyllum</i> sp.	Fabaceae	Patagonia	Leaves
<i>Hoffmannseggia</i> sp.	Fabaceae	Monte-Patagonia transition	Seed
<i>Lupinus</i> aff. <i>oreophilus</i>	Fabaceae	Patagonia	Leaves, Endocarp, leaves, stem
<i>Prosopis</i> sp.	Fabaceae	Monte	Leaves
<i>Balbisia gracilis</i>	Ledocarpaceae	Patagonia	Leaves
<i>Bromus</i> sp.	Poaceae	Patagonia	Anthercium
<i>Festuca</i> sp.	Poaceae	Patagonia	Bluegrass
<i>Hordeum</i> sp.	Poaceae	Patagonia	Bluegrass
<i>Jarava</i> sp.	Poaceae	Patagonia	Anthercium, bluegrass, endocarp
<i>Poa</i> sp.	Poaceae	Patagonia	Bluegrass
<i>Gilia crassifolia</i>	Polemoniaceae	Patagonia	Stem
<i>Acantholippia seriphioides</i>	Verbenaceae	Monte	Leaves, seed
<i>Junellia seriphioides</i>	Verbenaceae	Patagonia	Leaves, seed
aff. <i>Larrea</i>	Zigophyllaceae	Monte	Seed

seasonal climate regarding the precipitation regime.

An intensification of dry conditions is evident around 9.2 ka and prevailed during the mid-Holocene in the Huenul area according to the pollen record. Thus, mid-Holocene (6500–5500 cal yr BP) vegetation was similar to that of the early Holocene (particularly that between 9400 and 9200 cal yr BP), but Monte elements (e.g. *Prosopis*, *Larrea*) increase in abundance with the concomitant decrease of Monte-Patagonia transition elements such as *Schinus*, *Ephedra* and *Senecio* type. The latter implies an intensification of dry conditions that are supported by the percentages of Amaranthaceae, which are lower than before, probably indicating that wet/dry cycles were not as frequent as during the early Holocene. On the other hand, most mid-Holocene (9200, 6500 and 5500 cal yr BP) macrofossil assemblages are co-dominated by Monte and Monte-Patagonia transition taxa, which would imply an increase in moisture compared to the early Holocene. However, the values for richness and diversity of the assemblages are the lowest of the whole sequence, suggesting that environmental conditions around the Huenul locality would have been really unproductive. This matches the inferences made from the pollen record for this period reflecting the existence of the most pronounced dry conditions for Holocene at both local and regional scales.

Since ca. 4200 cal yr BP, Monte-Patagonia transition (*Ephedra*, *Senecio* type) and particularly Patagonia elements (*Baccharis* type, *Chuquiraga*, *Mulinum*, *Proustia* and *Nassauvia* type) increased their

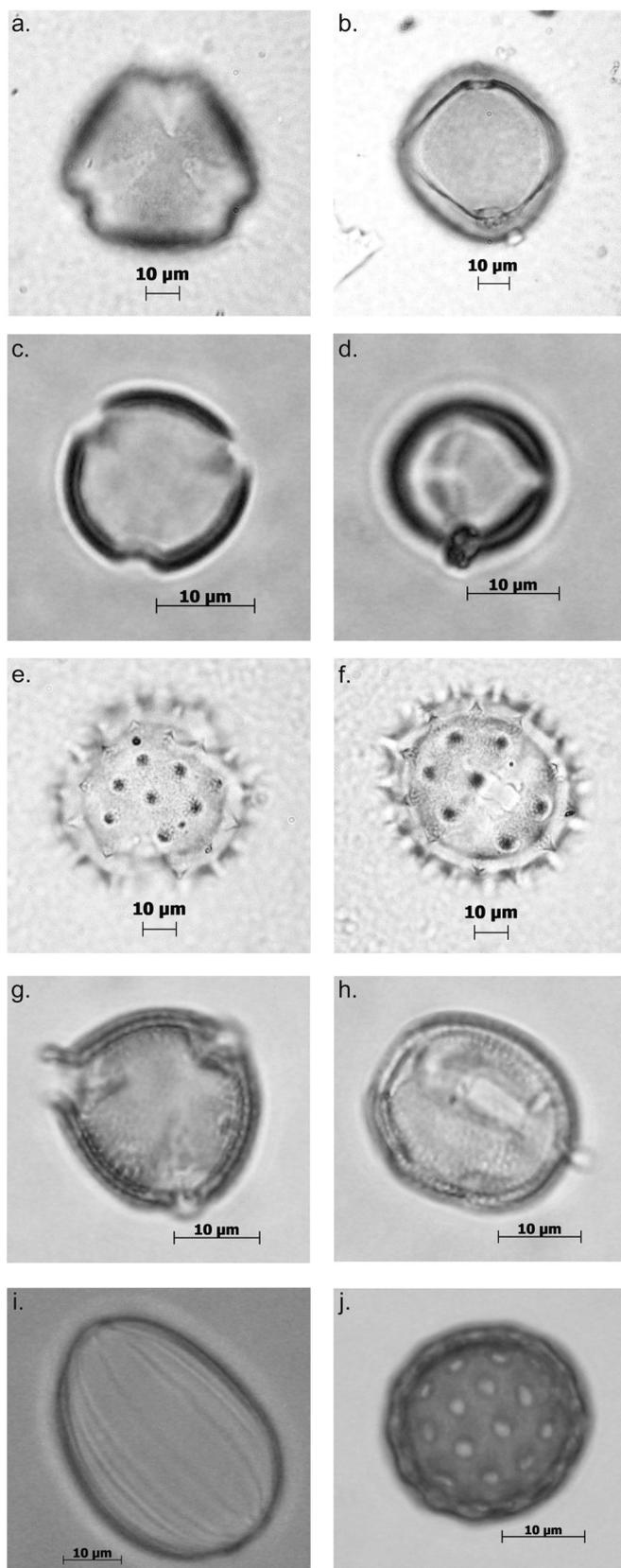


Fig. 6. Photographs of some pollen grains found in the Huenul rodent middens fossil assemblages (a) polar and (b) equatorial views of *Prosopis*; (c) polar and (d) equatorial views of *Larrea*; (e) polar and (f) equatorial views of Asteraceae subf. Asteroideae (*Senecio* type); (g) polar and (h) equatorial views of Fabaceae subf. Papilionoideae (*Adesmia* type); i. equatorial view of *Ephedra* and j. Amaranthaceae.

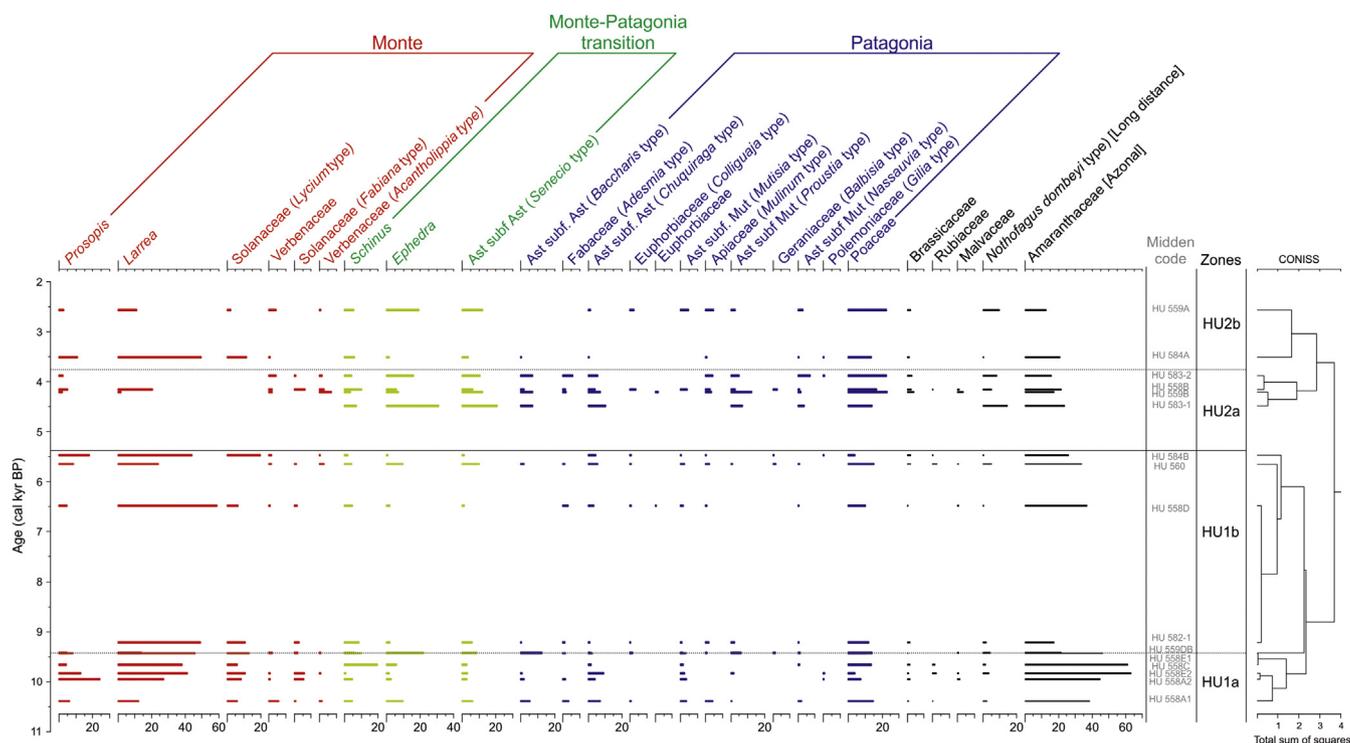


Fig. 7. Pollen diagram from Huenul rodent midden series in percentages showing the inferred climatic conditions: D⁺ much drier than present; D slightly drier than present; W⁺ much wetter than present; W slightly wetter than present.

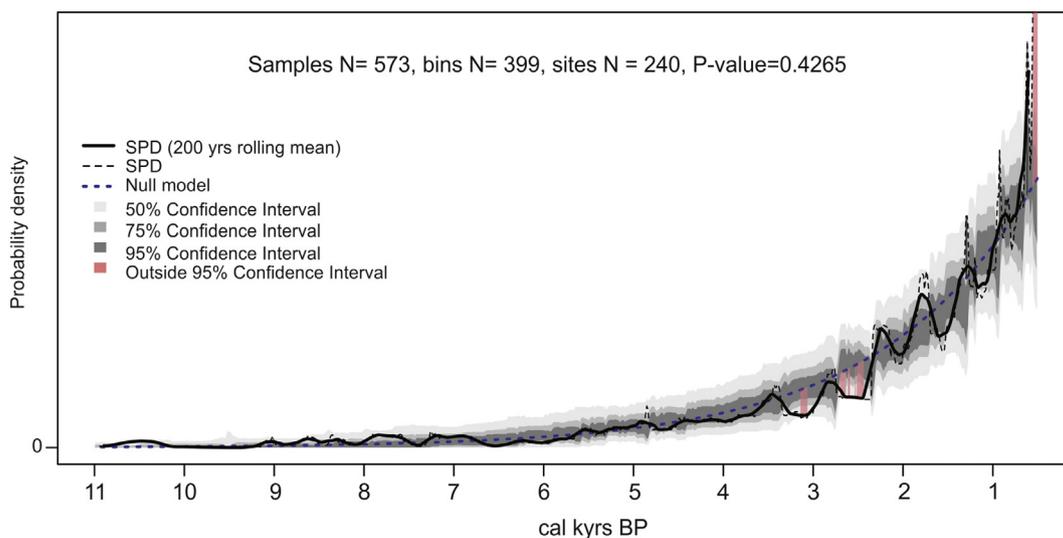


Fig. 8. Summed Probability Distribution (SPD) of the anthropogenic ¹⁴C database from the central-western South American deserts (data in Supplementary Material 2). No significant deviations from the null exponential model were detected.

percentages at the expense of Monte elements. Azonal plants percentages decreased while long distance taxa, such as *Nothofagus dombeyi*-type, increased up to 15%. This is the major change recorded in Huenul during the Holocene, reflecting that mid-Holocene dry conditions were followed by more humid scenarios than present. Amaranthaceae percentages did not surpass 20% indicating a reduction in the alternation of wet/dry conditions when compared to the previous period, while *Nothofagus dombeyi*-type, originated in the forests along the Andes, increased up to 15%, probably indicating an enhanced W-E pollen transport by surface winds related to the Southern Westerlies. Similar but more moderate humidity conditions prevailed during the late Holocene (3500–2500 cal yr BP), as indicated by an increase of percentages of Monte-Patagonia transition elements.

Macrofossil assemblages are co-dominated by Monte, Monte-Patagonia and Patagonia elements, suggesting an amelioration of moisture conditions in two distinct phases. Between 4200 and 3800 cal yr BP, the abundance of *Mulinum spinosum* and most of the grasses along with an increase in diversity indicate the most humid period of the Holocene, coinciding with the pollen record. Between 3500 and 2500 cal yr BP, the co-dominance of elements belonging to the three vegetation units along with a reduction of diversity and, particularly, the abundances of grasses, reveal slightly wetter conditions than present, but drier than the precedent period. In synthesis, both records reflect increased humidity at the local and regional scales during the late Holocene, which would result from an increase in winter precipitation due to a higher incidence of the Southern Westerlies.

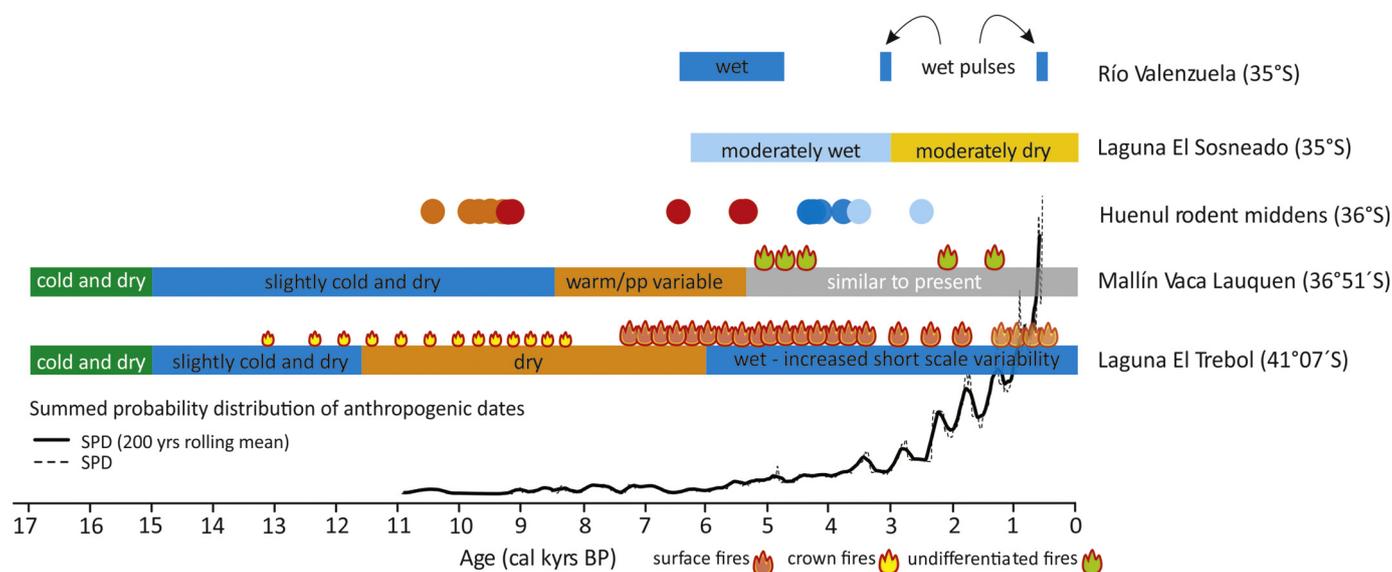


Fig. 9. Schematic comparison of midden data from the Huenul series (coloured circles) and the summed probability distribution (SPD) of the anthropogenic ^{14}C database at the regional scale with palaeoclimatic conditions inferred from previous surveys in northern Patagonia (Argentina) including Holocene glacial advances in Río Valenzuela (Espizúa, 2005; Espizúa and Pitte, 2009); the pollen record of Laguna El Sosneado (Navarro et al., 2012) and the pollen and charcoal records of Mallín Vaca Lauquen (Markgraf et al., 2008) and Laguna El Trébol (Whitlock et al., 2006).

5.4. Regional paleoclimatic integration

On a regional scale, the records from the lee side of the Andes [Mallín Vaca Lauquen (MVL), 36.5°S, Markgraf et al., 2008; Laguna El Trébol (LET), 41°S, Whitlock et al., 2006] showed cold and dry conditions during the late Glacial (17,000–15,000 cal yr BP) followed by a gradual increase of temperature but still under drier conditions than present, which lasted up to the Pleistocene-Holocene transition (15,000–11,500 cal yr BP; Fig. 9). While these conditions prevailed in MVL, the record from LET suggests drier conditions during the early Holocene (11,500–8000 cal yr BP) and the beginning of the mid-Holocene (8000–6000 cal yr BP), associated to an increased frequency of crown fires. Eastwards from these sites, the Huenul rodent midden series (HU) supports this latter climatic scenario reflecting drier than present conditions under a marked seasonal precipitation regime between 10,500–9400 cal yr BP (Fig. 9). Therefore, records from northern Patagonia show early Holocene dry conditions, a common and widespread pattern in southern South America at both sides of the Andes, which is likely a consequence of a weakened westerly flow (weaker Southern Westerlies) from mid to high latitudes (e.g. Whitlock et al., 2001, 2006; Abarzúa and Moreno, 2008; Iglesias et al., 2011; de Porras et al., 2012).

A synchronous change towards the amelioration of dry conditions was recorded at the regional scale across northern Patagonia during the mid-Holocene (8000–6500 cal yr BP; Fig. 9). Around 7500 cal yr BP, an increase in the frequency of fire episodes, along with a change in fire regime from crown to surface fires, was recorded at 41°S (LET; Whitlock et al., 2006; Fig. 9). These preceded the explosive development of Cupressaceae forest at this latitude associated to a change from dry to wet and highly variable conditions around 6000 cal yr BP. Northwards, the occurrence of Neoglacial advances at Río Valenzuela basin (35°S; Espizúa, 2005; Espizúa and Pitte, 2009), as well as an increase of humidity indicators in Laguna El Sosneado (LES) pollen record (35°S; Navarro et al., 2012), point out the establishment of wet conditions since 6500 cal yr BP (Fig. 9). The HU midden record actually indicates that early Holocene dry conditions intensified during the mid-Holocene followed by the onset of a trend towards the most humid conditions of the Holocene, which took place during the late Holocene (Fig. 9). This difference could be related to the eastward position of the HU locality regarding the W-E precipitation gradient where (1) the moisture

threshold for vegetation to change may be higher, and/or (2) there could be a time lag in the moisture increase.

At a wider spatial scale, terrestrial paleoclimatic records north of 50°S indicate a multi-millennial rise in the intensity of the Southern Westerlies starting at 9000–7800 cal yr BP associated with colder (and/or wetter) conditions than those prevailing during the early Holocene (e.g. Whitlock et al., 2001, 2006; Abarzúa and Moreno, 2008; Iglesias et al., 2011; de Porras et al., 2012). Coupled ocean-atmosphere models revealed that there is a small but consistent equatorward shift of 30° in the latitude of maximum wind speed over the entire SH, due to increased/decreased insolation during the transitional seasons SON/MAM, which results in a small increase of wind speed over the South Pacific north of 50°S (Rojas and Moreno, 2011).

The late Holocene was characterized by highly variable climatic conditions across northern Patagonia, which remained relatively similar to those described after 6000 cal yr BP for the southernmost area (> 36°S; Fig. 9). The northernmost (< 35°S) records, on the other hand, reflected Neoglacial advances between 6400 and 4800 cal yr BP (RV, 35°S; Espizúa, 2005; Espizúa and Pitte, 2009) coinciding with the most humid conditions at HU area around 4500 cal yr BP, followed by a reduction of humidity between 3500 and 2500 cal yr BP (Fig. 9). In contrast, the pollen record of LES (35°S; Navarro et al., 2012) shows a change towards moderately drier conditions up to the present (Fig. 9). Widespread wetter conditions during the late Holocene may be attributable to intensified westerly flow since 6000 BP at the centennial-millennial scales associated to the onset of El Niño-like inter-annual variability (Whitlock et al., 2006; Abarzúa and Moreno, 2008; Iglesias et al., 2011).

5.5. Climate change and human occupations in the SAAD

The diachronic analysis of anthropogenic radiocarbon dates from the central-western area of the SAAD at 36°S conforms to a fitted exponential model of steady background population growth and taphonomic loss, not suggesting significant demographic changes that may have been the result of the impact of climate change. Given the size of our database and the power of the methods used, and against previous interpretations (Barberena et al., 2017), we cannot attribute the fluctuations in the observed SPD to demographic events (see also Perez et al., 2016; Gordón et al., 2019), which may instead represent artifacts

of small sample size and/or calibration. Significantly, this includes the mid-Holocene, for which there is considerable debate regarding the existence of archaeological hiatuses or troughs (Gil et al., 2005; Neme and Gil, 2009; García, 2010; Méndez et al., 2015; Durán et al., 2016; Barberena et al., 2017). The local paleoecological results and macro-regional synthesis presented here simultaneously signal that the most arid conditions took place during the mid-Holocene. While the effect of small sample size of the radiocarbon database cannot be yet discarded, it is not possible to tie this dry period to significant demographic shifts in this large part of the SAAD. However, there are changes in the spatial distribution of archaeological sites across the landscape suggesting that significant rearrangements in the scale and/or patterns of mobility would have occurred (Garvey, 2008; Neme and Gil, 2009; Méndez et al., 2015). While it remains as a distinct possibility that the most arid tracts of the landscape were either abandoned or occupied only as 'passing-through places' (sensu Veth, 1993), the macro-regional trend inferred from the SPD suggests that human populations occupying the central-western part of the SAAD coped with the mid-Holocene arid period successfully from a demographic perspective. This may have been achieved by relocating in space (Méndez et al., 2015), changing settlement and subsistence patterns (Veth, 2005; Garvey, 2008), extending interaction networks (Fitzhugh et al., 2011; Romero Villanueva et al., 2020), producing technological innovations or combinations thereof.

Interestingly, significant demographic declines have been associated with climate change during the mid-Holocene at a continental scale of analysis (Riris and Arroyo-Kalin, 2019; see also Goldberg et al., 2016). As Riris and Arroyo-Kalin suggest (2019:6), "the demographic signals highlighted on a broad [continental] scale in this work are composites of local archaeological records". This provides a productive platform to study under what socio-ecological conditions human societies are able to successfully build resilience or not (Easdale et al., 2016; Fitzhugh et al., 2016).

6. Conclusions

Pollen and macrofossil evidence from the Huenul series rodent midden records reflect subtle vegetation changes driven by climatic variability at millennial timescale. Drier than present environmental conditions prevailed during the early Holocene peaking during the mid-Holocene, followed by wetter than present scenarios during the late Holocene in two different phases. These environmental and climatic dynamics are in complete agreement to those recorded from other paleoclimatic records from northern Patagonia, with the exception of the mid-Holocene, hence suggesting a common mechanism associated to precipitation dynamics related to the Southern Westerlies. Our results demonstrate the potential of rodent middens as records of past environmental and climatic changes along arid and semiarid areas of SAAD.

The comparison of paleoecological trends with human demographic trajectories as inferred from the distribution of radiocarbon dates does not suggest climate-related adjustments by human societies inhabiting this part of the SAAD. While more evidence is still needed, this case would represent a successful human adaptation to enhanced arid conditions in this part of the SAAD. This regional trend does not coincide with a scenario of mid-Holocene demographic decline recently presented for South America at large (Goldberg et al., 2016; Riris and Arroyo-Kalin, 2019). However, this apparent contradiction may only suggest the existence of diverse regional socio-demographic trajectories underlying continental trends. We look forward to advance developing a multi-scalar interdisciplinary research framework for the analysis of climate change and human resilience in the South American drylands.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.109894>.

References

- Abarzúa, A.M., Moreno, P.I., 2008. Changing fire regimes in the temperate rainforest region of southern Chile over the last 16,000 yr. *Quat. Res.* 69, 62–71.
- Barberena, R., 2015. Cueva Huenul 1 archaeological site, Northwestern Patagonia, Argentina: initial colonization and mid-Holocene demographic retraction. *Lat. Am. Antiq.* 26, 304–318.
- Barberena, R., Borrazzo, K., Rughini, A.A., Romero, G., Pompei, M.P., Llano, C., de Porras, M.E., Durán, V., Stern, C., Re, A., Estrella, D., Forasiépi, A., Fernández, F., Chidiak, M., Acuña, L., Gasco, A., Quiroga, M.N., 2015a. Perspectivas arqueológicas para Patagonia septentrional: sitio Cueva Huenul 1 (provincia del Neuquén, Argentina). *Magallania* 43, 137–163.
- Barberena, R., Prates, L., de Porras, M.E., 2015b. The human occupation of northwestern Patagonia (Argentina): paleoecological and chronological trends. *Quat. Int.* 356, 111–126.
- Barberena, R., Méndez, C., de Porras, M.E., 2017. Zooming out from archaeological discontinuities: the meaning of mid-Holocene temporal troughs in South American deserts. *J. Anthropol. Archaeol.* 46, 68–81.
- Beltrame, M., de Porras, M.E., Barberena, R., Llano, C., Sardella, N., 2016. First study of fossil rodent middens as source of paleoparasitological evidences (northwestern Patagonia, Argentina). *Parasitol. Int.* 65, 352–356.
- Betancourt, J., Saavedra, B., 2002. Paleomadrigueras de roedores, un nuevo método para el estudio del Cuaternario en zonas áridas de Sudamérica. *Rev. Chil. Hist. Nat.* (3), 527–546.
- Betancourt, J., Van Devender, T., Martin, P., 1990. *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson.
- 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.
- Chase, B., Boom, A., Carr, A., Meadows, M., Reimer, P., 2013. Holocene climate change in southernmost South Africa: rock hyrax middens record shifts in the southern westerlies. *Quat. Sci. Rev.* 82, 199–205.
- Chiapella, J., Ezcurra, C., 1999. La flora del parque provincial Tromen, provincia de Neuquén, Argentina. *Multequina* 8, 51–60.
- Durán, V., Winocur, D., Stern, C., Garvey, R., Barberena, R., Peña Monné, J.L., Benítez, A., 2016. Impacto del volcanismo y glaciarrismo holocénicos en el poblamiento humano de la cordillera sur de Mendoza (Argentina): una perspectiva geoarqueológica. *Intersecciones en Antropología* 4, 33–46 Volumen Especial.
- Easdale, M.H., Aguiar, M.R., Paz, R., 2016. A social-ecological network analysis of Argentinean Andes transhumant pastoralism. *Reg. Environ. Chang.* 16, 2243–2252. <https://doi.org/10.1007/s10113-015-0917-8>.
- Esau, K., 1960. Anatomy of seed plants. *Soil Sci.* 90 (2), 149. <https://doi.org/10.1097/000110694-196008000-00031>.
- Espizúa, L., 2005. Holocene glacier chronology of Valenzuela Valley, Mendoza. *The Holocene* 15, 1079–1085.
- Espizúa, L., Pitte, P., 2009. The Little Ice Age glacier advance in the Central Andes (35°S), Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 281, 345–350.
- Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*. John Wiley, Chichester.
- Fernández, F.J., Teta, P., Barberena, P., Pardiñas, U.F.J., 2012. U.F.J. 2012. Small mammal remains from Cueva Huenul 1, northern Patagonia, Argentina. *Taphonomy and paleoenvironments since the Late Pleistocene. Quaternary International* 278, 22–31.

- Fernández, F.J., Ballejo, F., Moreira, G.J., Tonni, E.P., De Santis, L.J.M., 2015. Roedores cricétidos de la Provincia de Mendoza Guía cráneo-dentaria orientada para su aplicación en estudios zooarqueológicos. Sociedad Argentina de Antropología, Buenos Aires.
- Fernández, M.V., Barberena, R., Rughini, A., Giesso, M., Durán, V.A., Cortegoso, V., Borrazzo, K., Lucero, G., Romero Villanueva, G., Garvey, R., Macdonald, B.L., Glascock, M.D., 2017. Obsidian geochemistry, geoaerchaeology, and lithic technology in northern Patagonia (Argentina). *Journal of Archaeological Science: Reports* 13 (2), 372–381.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas. *International Journal of Climatology* 37 (12), 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Fitzhugh, B., Phillips, S.C., Gjesfeld, E., 2011. Modeling hunter-gatherer information networks: An archaeological case study from the Kuril Islands. In: Whallon, R., Lovis, W.A., Hitchcock, R.K. (Eds.), *Information and Its Role in Hunter-gatherer Bands*. University of California Press, Los Angeles, pp. 85–115.
- Fitzhugh, B., Gjesfeld, E.W., Brown, W.A., Hudson, M.J., Shaw, J.D., 2016. Resilience and the population history of the Kuril Islands, Northwest Pacific: a study in complex human ecodynamics. *Quat. Int.* 419, 165–193. <https://doi.org/10.1016/j.quaint.2016.02.003>.
- Galende, G.I., Raffaele, E., 2012. Diet selection of the southern vizcacha (*Lagidium viscacia*): a rock specialist in north western Patagonian steppe, Argentina. *Acta Theriol.* 57, 333–341.
- Galende, G., Grigera, D., von Thüngen, J., 1998. Composición de la dieta del chinchillón (*Lagidium viscacia*, Chinchillidae) en el noroeste de la Patagonia. *Mastozool. Neotrop.* 5, 123–128.
- García, A., 2010. Human occupation during the Mid-Holocene in Western Argentina: a comment on Neme and Gil. *Curr. Anthropol.* 51 (3), 415–416.
- Garreaud, R., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day south american climate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 281, 180–195.
- Garvey, R., 2008. A behavioural ecological approach to a proposed middle Holocene occupational gap. *Before Farming* 2008 (2).
- Gil, A., Zárate, M., Neme, G., 2005. Mid-Holocene paleoenvironments and the archaeological record of Southern Mendoza, Argentina. *Quat. Int.* 132, 81–94.
- Gil, A.F., Giardina, M.A., Neme, G.A., Ugan, A., 2014. Demografía humana e incorporación de cultígenos en el centro occidente argentino: explorando tendencias en las fechas radiocarbónicas. *Revista Española de Antropología Americana* 44 (2), 523–553.
- Goldberg, A., Mychajliw, A.M., Hadly, E.A., 2016. Post-invasion demography of pre-historic humans in South America. *Nature* 532 (7598), 232–235.
- Gordón, F., Beguelin, M., Rindel, D.D., Della Negra, C., Hajduk, A., Vázquez, R.C., Cobos, V.A., Perez, S.I., Bernal, V., 2019. Estructura espacial y dinámica temporal de la ocupación humana de Neuquén (Patagonia argentina) durante el Pleistoceno final-Holoceno. *Intersecciones en Antropología* 20 (1), 93–105.
- Gourou, P., Papy, L., 1966. Compendio de geografía general. Ediciones RIALP, Madrid.
- Grimm, E., 1987. CONISS: a fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Comput. Geosci.* 5, 13–35.
- Grimm, E.M., 2011. Interannual climate variability in South America: impacts on seasonal precipitation, extreme events, and possible effects of climate change. *Stoch. Env. Res. Risk* A. 25 (4), 537–554.
- Grosjean, M., Cartajena, I., Geyh, M.A., Núñez, L., 2003. From proxy data to paleoclimate interpretation: the mid-Holocene paradox of the Atacama Desert, northern Chile. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 194, 247–258.
- Heusser, C., 1971. *Pollen Spores of Chile*. University of Arizona Press, Tucson.
- Hofreiter, M., Betancourt, J., Pelliza Striller, A., Markgraf, V., McDonald, G., 2003. Phylogeny, diet, and habitat of an extinct ground sloth from. *Quat. Res.* 59, 364–378.
- 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., Turney, C.S., Zimmerman, S.R.H., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.
- Iglesias, V., Whitlock, C., Bianchi, M.M., Villarrosa, G., Outes, V., 2011. Holocene climate variability and environmental history at the Patagonian forest/steppe ecotone: Lago Mosquito (42°29'37.89"S, 71°24'14.57"W) and Laguna del Cóndor (42°20'47.22"S, 71°17'07.62"W). *The Holocene* 22, 1297–1307.
- Kiesling, R., 1984. Estudios en Cactaceae de Argentina: *Maihueniopsis*, *Tephrocactus* y géneros afines (Opuntioideae). *Darwiniana* 25 (1), 171–215.
- Latorre, C., Betancourt, J.L., Rylander, K.A., Quade, J., 2002. Vegetation invasions into absolute desert: a 45; th000 yr rodent midden record from the Calama-Salar de Atacama basins, northern Chile (lat 22–24 S). *Geol. Soc. Am. Bull.* 114, 349–366.
- Latorre, C., Betancourt, J.L., Rylander, K.A., Quade, J.J., Matthei, O., 2003. A vegetation history from the arid prepuna of northern Chile (22–23 S) over the last 13 500 years. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 194, 223–246.
- Latorre, C., Santoro, C.M., Ugalde, P.C., Gayo, E.M., Osorio, D., Salas-Egaña, C., De Pol-Holz, R., Joly, D., Rech, J.A., 2013. Late Pleistocene human occupation of the hyperarid core in the Atacama Desert, northern Chile. *Quat. Sci. Rev.* 77, 19–30.
- León, R., Bran, D., Collantes, M., Paruelo, J., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecol. Austral* 8, 125–144.
- Llano, C., Sosa, P., Sánchez, C., Barberena, R., 2017. Arqueobotánica de Cueva Huenul 1 (Neuquén, Argentina): Selección y procesamiento de especies vegetales. *Intersecciones en Antropología* 20 (2), 211–223.
- 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). *J. Quat. Sci.* 20, 493–507.
- Markgraf, V., 1987. Paleoenvironmental changes at the northern limit of the subantarctic Nothofagus forest, lat 37°S, Argentina. *Quat. Res.* 28, 119–129.
- Markgraf, V., D'Antoni, H.L., 1978. Pollen Flora of Argentina: Modern Spore and Pollen Types of Pteridophyta, Gymnospermae, and Angiospermae. University of Arizona Press, Tucson, pp. 208.
- Markgraf, V., Betancourt, J., Rylander, K.A., 1997. Late-Holocene rodent middens from Rio Limay, Neuquen Province, Argentina. *The Holocene* 7, 325–329.
- Markgraf, V., Whitlock, C., Anderson, S., García, A., 2008. Late Quaternary vegetation and fire history in the northernmost Nothofagus forest region: Mallín Vaca Lauquen, Neuquén Province, Argentina. *J. Quat. Sci.* 24, 248–258.
- Martin, A., Barkley, W., 1973. *Seed Identification Manual*. University of California Press, New Jersey (220 pp.).
- Méndez, C., Gil, A., Neme, G., Delaunay, A.N., Cortegoso, V., Huidobro, C., Durán, V., Maldonado, A., 2015. Mid Holocene radiocarbon ages in the Subtropical Andes (~29°–35° S), climatic change and implications for human space organization. *Quat. Int.* 356, 15–26.
- Navarro, D., Rojo, L., De Francesco, C., Hassan, G., 2012. Paleocología y reconstrucciones paleoambientales en Mendoza durante el Holoceno. In: Neme, G., Gil, A. (Eds.), *Paleocología humana en el sur de Mendoza: perspectivas arqueológicas*. Sociedad Argentina de Antropología, Buenos Aires, pp. 17–56.
- Neme, G., Gil, A., 2009. Human occupation and increasing Mid-Holocene Aridity. Southern Andean perspectives. *Curr. Anthropol.* 50, 149–163.
- Núñez, L., Santoro, C., 1988. Cazadores de la Puna Seca y Salada del área Centro-Sur Andina (Norte de Chile). *Atacameños Stud.* (9), 11–60.
- Oyarzabal, M., Clavijo, J., Oakley, L., Biganzoli, F., Tognetti, P., Barberis, I., Maturó, H.M., Aragón, R., Campanello, P.I., Prado, D., Oesterheld, M., León, R.J.C., 2018. Unidades de vegetación de la Argentina. *Ecología Austral* 28 (1), 40–63.
- Palacios, R.A., Bravo, L.D., 1974-1975. Estudio morfológico de las semillas de *Prosopis*, II: Algunas especies Norteamericanas y Neotropicales. *Darwiniana* 19, 357–372.
- Pardiñas, U.F.J., D'Elía, G. (Eds.), 2015. *Mammals of South America. Volume 2: Rodents*. University of Chicago Press, Chicago.
- Passera, C.B., Borsetto, O., 1989. Aspectos ecológicos de *Atriplex lampa*. *Investigación Agraria. Plant Prod. Prot.* 4 (2), 179–198.
- Perez, S.I., Postillone, M.B., Rindel, D., Gobbo, D., Gonzalez, P.N., Bernal, V., 2016. Peopling time, spatial occupation and demography of Late Pleistocene–Holocene human population from Patagonia. *Quat. Int.* 425, 214–223.
- de Porras, M.E., Maldonado, A., Abarzúa, A.M., Cárdenas, M.L., Francois, J.P., Martel-Cea, A.J., Stern, C.R., Méndez, C., Reyes, O., 2012. Postglacial vegetation, fire and climate dynamics at Central Chilean Patagonia (Lake Shaman, 44°S). *Quat. Sci. Rev.* 50, 71–85.
- de Porras, M.E., Maldonado, A., De Pol-Holz, R., Latorre, C., Betancourt, J.L., 2017. Late Quaternary environmental dynamics in the Atacama Desert reconstructed from rodent midden pollen records. *J. Quat. Sci.* 32, 665–684.
- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna URL. <http://www.R-project.org/>.
- Redford, K.H., Eisenberg, J.F., 1992. *Mammals of the Neotropics: The Southern Cone*. The University of Chicago Press, Chicago.
- Riris, P., Arroyo-Kalin, M., 2019. Widespread population decline in South America correlates with mid-Holocene climate change. *Sci. Rep.* 9 (1), 6850.
- Rojas, M.I., Moreno, P.I., 2011. Atmospheric circulation changes and neoglaciation conditions in the Southern Hemisphere mid-latitudes: insights from PMIP2 simulations at 6 kyr. *Clim. Dyn.* 37, 357–375.
- Romero Villanueva, G., Barberena, R., 2017. Los huesos de guanaco pintados de Cueva Huenul 1 (norte del Neuquén, Patagonia septentrional). *Relaciones de la Sociedad Argentina de Antropología XLII* 3, 369–377.
- Romero Villanueva, G., Lucero, G., Barberena, R., 2020. 'Andean summer-break': rock art insights on information networks and social interaction in a desert-highland interface in northern Patagonia (South America). *Prehist. Art Notebooks* 1, 89–121 Número Especial.
- Rughini, A., Romero Villanueva, G., Lucero, G., Cardillo, M., Borrazzo, K., Fernández, M.V., Brera, A., Frigolé, C., Castillo, A., Vitores, M., Llano, C., Garvey, R., Barberena, R., 2020. Arqueología distribucional y biogeografía humana en un paisaje andino-patagónico. *Lat. Am. Antiq.* <https://doi.org/10.1017/laq.2020.22>. (in press).
- Schwarz, G., 1978. Estimating the dimension of a model. *Ann. Stat.* 6 (2), 461–464.
- Shennan, S., Downey, S.S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., Manning, K., Thomas, M.G., 2013. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* 4, 2486.
- Spaulding, G., Betancourt, J., Croft, L., Cole, K., 1990. *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson (469 pp.).
- Spotorno, A.E., Patton, J.L., 2015. Superfamily Chinchilloidea Bennett, 1833. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), *Mammals of South America Volume 2: Rodents*. University of Chicago Press, Chicago, pp. 762–783.
- Hugot, J.P., Sutton, C.A., 1989. Contribution a La Connaissance de La Faune Parasitaire d'Argentine, XV. Etude Morphologique de Heteroxyrema (Cavioxyura) Viscaciae n. Sp. (Nematoda, Heteroxyrenematidae) Parasite de Lagidium Viscacia Boxi (Mammalia, Rodentia). *Systematic Parasitology* 13 (2), 111–120. <https://doi.org/10.1007/BF00015219>.
- Timpson, A., Barberena, R., Méndez, C., Thomas, M.G., Manning, K., 2020. Directly modelling population change in the South American Arid Diagonal using 14C dates. *Philos. Trans. R. Soc. B* (in press).
- Veth, P.M., 1993. Islands in the interior. The dynamics of prehistoric adaptations within the Arid Zone of Australia. *International monographs in prehistory*. In: Archaeological Series 3. Berghahn (Ann Arbor).
- Veth, P.M., 2005. Cycles of aridity and human mobility: risk minimization among late Pleistocene Foragers of the Western Desert, Australia. In: Veth, P., Smith, M., Hiscock, P. (Eds.), *Desert Peoples. Archaeological Perspectives*. Blackwell, Oxford, pp. 100–115.
- Viale, M., Bianchi, E., Cara, L., Ruiz, L.E., Villalba, R., Pitte, P., Masiokas, M., Rivera, J., Zalazar, L., 2019. Contrasting climates at both sides of the Andes in Argentina and

- Chile. *Front. Environ. Sci.* 7, 69. <https://doi.org/10.3389/fenvs.2019.00069>.
- Villagrán, C., Varela, J., 1990. Palynological evidence for increased aridity on the Central Chilean coast during the Holocene. *Quat. Res.* 34, 198–207.
- Walker, S.R., Ackerman, G., Schachter-Broide, J., Pancotto, V., Novaro, A.J., 2000. Habitat use by mountain vizcachas (*Lagidium viscacia* Molina, 1782) in the Patagonia steppe. *Mamm. Biol.* 65, 293–300.
- Whitlock, C., Bartlein, P.J., Markgraf, V., Ashworth, A.C., 2001. The midlatitudes of North and South America during the Last Glacial Maximum and early Holocene: similar paleoclimatic sequences despite differing largescale controls. In: Markgraf, V. (Ed.), *Interhemispheric Climate Linkages: Present and Past Interhemispheric Climate Linkages in the Americas and Their Societal Effects*. Academic Press, New York, pp. 391–416.
- Whitlock, C., Bianchi, M., Bartlein, P., Markgraf, V., Marlon, J., Walsh, M., McCoy, N., 2006. Postglacial vegetation, climate, and fire history along the east side of the Andes (lat 41–42.5 S), Argentina. *Quat. Res.* 66 (2), 187–201.
- Williams, A.N., Ulm, S., Cook, A.R., Langley, M.C., Collard, M., 2013. Human refugia in Australia during the Last Glacial Maximum and Terminal Pleistocene: a geospatial analysis of the 25–12 ka Australian archaeological record. *J. Archaeol. Sci.* 40 (12), 4612–4625.