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 ^{14}C 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

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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 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

75 the arid and semi-arid areas of the SAAD that contribute to this research topic (e.g. Betancourt et

76 al., 2000; Maldonado et al., 2005; de Porras et al., 2017).

77 Fossil rodent middens are complex accumulations of local vegetation, nesting materials,

78 insect remains, bones, sediment and feces, preserved underneath rock slabs and within caves, that

79 provide an excellent paleoecological archive of desert ecosystems (e.g., Betancourt et al., 1990,

80 2000; Latorre et al., 2003; Maldonado et al., 2005; Chase et al., 2013; de Porras et al. 2017).

81 Previous evidence indicates that these deposits have been built in South America over the last

82 50,000 years or more, by four families of rodents (Abrocomidae, Chinchillidae, Muridae, and

83 Octodontidae). While the widespread presence of these deposits across the SAAD is well-

84 documented (Betancourt and Saavedra, 2002; see also Markgraf et al., 1997; Hofreiter et al., 2003),

85 these fossil deposits have not been systematically studied eastwards of the Andes. Rodent middens

86 provide fundamental archives in arid and semiarid areas of northwestern Patagonia, since standard

87 sedimentary environments (lakes, fens) are usually temporary, and largely desiccated during the

88 summer. Hence, there is a large and still unexploited analytical potential in these fossil deposits.

89 In this paper we present the results of an interdisciplinary project seeking to reconstruct

90 changes in vegetation, climate, and human presence in drylands of northwestern Patagonia since

91 the early Holocene times. We deploy a multi-scalar approach. First we present local scale fossil

92 rodent midden data (plant macrofossil, pollen, and paleoparasite records) from the Huenul study

93 site in Neuquén Province, Argentina (36°57'S,69°49'W; 1000 masl), located in the Monte drylands

94 close to the ecotone with more humid Patagonian vegetation (Fig. 1). Second, we develop an

95 interdisciplinary approach, combining fossil rodent midden data with a regional program of

96 archaeological survey and excavation aimed to determine the timing and biogeographic pattern of

97 human occupation of the northern Patagonian deserts (Barberena, 2015; Barberena et al., 2015a;

98 Beltrame et al., 2016; Rughini et al., 2020). Significantly, the Huenul study site provides a sequence

99 of fossil rodent middens associated to the archaeological archive of Cueva Huenul 1 site, which

100 provides evidence of a discontinuous human occupation since the Pleistocene-Holocene transition

101 (Barberena, 2015; Barberena et al., 2015b). Thirdly, we move on to regional and macro-regional

102 scale by integrating available paleoecological and archaeological evidence. The temporal

103 fluctuations in human presence in the drylands are analyzed by using ^{14}C dates from archaeological

104 contexts as a proxy of density of human occupation (Shennan et al., 2013; Williams et al., 2013;

105 Timpson et al., 2015, 2020). On this basis, we reassess the previous suggestions about the impact

106 of climate change on human populations throughout the Holocene.

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110 ## 2. Ecological and paleoecological background
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113 *2.1 Modern setting*

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115 Northwestern semiarid Patagonia (36-37°S; 69-70°W; Neuquén province) lies on the eastern side

116 of the Andes near the western limit of the SAAD at 36°S (Fig. 1a). The Andes function as a

117 topographic barrier to the prevailing westerly storm tracks, affecting the patterns of atmospheric

118 circulation and imposing a steep west-east gradient on precipitation and effective moisture

119 (Garreaud et al., 2009). Annual precipitation varies from ca. 1100 mm close to the current

120 Argentina-Chile border to 200-150 mm in the core of the SAAD at 36°S (Gourou and Papy, 1966;

121 Fig. 1a). Most of the precipitation (~75%) falls during winter associated to moisture sourced from

122 the Pacific Ocean brought by the Southern Westerlies system (Viale et al., 2019), while summer

123 precipitation related to Atlantic moisture is negligible in this area (Fig. 1b).

124 Vegetation distribution follows this precipitation gradient, from forest communities west

125 of the Andes (Chile) and confined to the Andean slopes in Argentina, giving way eastwards to the

126 grass-steppes of the Patagonia Province, characterized by a low shrubby steppe intermingled with

127 tussock grasses (Fig. 1c). The Poaceae family is prevalent in its floristic composition and the genus

128 *Stipa* is dominant. Other significant components of the grass flora are *Poa, Festuca*, and *Bromus*.

129 Shrubs with cushion-like appearance physiognomically characterize large areas. The most frequent

130 shrub species are *Chuquiraga* spp., *Colliguaja intergerrima, Azorella prolifera, Senecio*

131 *filaginoides*, *Berberis heterophylla*, *Baccharis darwinii, Anarthrophyllum rigidum, Nassauvia*

glomerulosa, Lycium chilense and *Trevoa patagonica* (Chiapella 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, *Bouganvillea spinosa* and *Schinus polygamus*, dwarf shrubs (e.g. *Accantholippia*

seriphioides, *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 chiloensis*, *Nassauvia*

glomerulosa, *Tetraglochin ameghinoi* and *Chuquiraga avellanedae* (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 (whilst 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 6400-4800 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; 1000-1050masl; 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

190 split along clear stratigraphic units where recognizable. Each midden was separated in the

191 laboratory into to subsamples to perform the plant macrofossil and pollen analysis (Fig. 2b). Fecal

192 pellets were taken from the plant macrofossil subsample from each midden for parasite analysis

193 and for radiocarbon dating by AMS and conventional methods (see details below).

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195 *3.2 Radiocarbon dating of the middens and phase model comparison with human occupations*
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197 The age of each midden was obtained through ^{14}C AMS or conventional radiocarbon dates

198 performed on 3 to 10 g of fecal pellets. The radiocarbon dates were calibrated to calendar years BP

199 using the SHCal13 calibration curve for the Southern Hemisphere (Hogg et al., 2013) using bespoke

200 scripts in R (R Core Team 2014).

201 To test if rodent and human occupations in the Huenul area (local scale) were concurrent

202 or mutually exclusive, we innovate a formal model comparison approach. The null hypothesis

203 (model 0) defines a concurrent presence of humans and rodents and therefore assumes all 32 ^{14}C

204 dates (16 anthropogenic and 16 from rodent middens) are random samples from a single continuous

205 phase between 12,000 and 300 cal yr BP. Model 1 introduces a single parameter (the date of a

206 phase boundary) which separates this time span into two phases, an exclusively human phase

207 followed by an exclusively rodent phase (human – rodent). Model 2 comprises two date parameters

208 to create three mutually exclusive phases (human – rodent – human). We continue in this way up

209 to and including model 7, with each subsequent model potentially fitting closer to the data but

210 requiring a greater number of parameters to achieve this. We assess the balance between this

211 goodness of fit and model complexity using the Bayesian Information Criterion (BIC) (Schwarz,

212 1978). Further methodological detail is provided in the Supplementary Material S1.

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214 *3.3 Analysis of paleoparasites, macro-botanical remains and pollen*
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216 The paleoparasitological study performed on rodent fecal pellets included samples of the

217 16 rodent middens, ten of which have been previously analyzed (Beltrame et al., 2016). Five fecal

218 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 10L 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 1-8x 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 *Maihueniopsis*, given its wide distribution

encompassing more than one biogeographic unit (Kiesling, 1984) and *Atriplex*, considered as

244 azonal vegetation related to saline soils mostly related to desiccation in the study area (Passera and

245 Borsetto, 1989).

246   The pollen analysis subsamples were hydrated 24-48 hours and sieved through a 120μm

247 mesh to separate macro- (plant, seeds, feces, etc.) and micro-remains (midden matrix), and a 1cm^3

248 aliquot of the micro-remains from each midden was processed following standard methods for

249 pollen extraction (Faegri and Iversen, 1989). At least 300 pollen grains were counted for each sample

250 which were identified based on the reference collection of Laboratorio de Paleoecología y

251 Paleoclima (CEAZA) and published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978).

252 Amaranthaceae and *Nothofagus* (*dombeyi* type) were excluded from the basic pollen sum, given that

253 the first one corresponds to azonal vegetation growing within a perennial stream close to the Huenul

254 locality and the second one is a long-distance pollen type produced by sub-Antarctic forests located

255 westwards in the Andes. A Constrained Incremental Sum of Squares (CONISS) cluster analysis

256 (Grimm, 1987) was performed to divide the fossil midden sequences into zones, considering all

257 pollen taxa included into the basic sum and contributing >2%.

258   Pollen percentages, CONISS cluster analysis and pollen and plant macrofossil diagrams

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

260   The interpretation of the pollen and macro-botanical remains records was carried out

261 considering that the Huenul locality is currently located at the Monte-Patagonia transition (Fig. 1c).

262 According to the regional relationships between precipitation and vegetation gradients (see Modern

263 Setting section), an increase in pollen percentages or RAI values of Monte taxa (Patagonian taxa)

264 would mean a decrease (increase) of moisture. Therefore, a qualitative artificial moisture scale was

265 created: D (drier than present), D$^+$ (slightly drier than present), W (slightly wetter than present) and

266 W$^+$ (much wetter than present).

267
268 *3.4 Temporal fluctuations in human populations*
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270   We assemble a database comprising 580 radiocarbon dates from 244 archaeological sites

271 from the central-western part of the SAAD (32°-40°S, Mendoza and Neuquén provinces;

272 Argentina) by merging and updating previous compilations (Supplementary Material S2; Barberena

273   et al., 2015a; Gil et al., 2015; Gordón et al., 2019). On this basis, we reconstruct human population

274   fluctuations through time using a Summed Probability Distribution (SPD), and test for significant

275   fluctuations from a null exponential distribution following an established approach which compares

276   the observed SPD with simulated SPDs generated under a null model of long-term exponential

277   demographic growth and taphonomic loss (Shennan et al., 2013). This approach can identify

278   unusual fluctuations through time that significantly depart from the null model, from which past

279   demographic events can be inferred. Further methodological detail is provided in Supplementary

280   Material S1.

4. Results

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

285
286   The sequence of radiocarbon dates at Huenul is composed of 32 samples across a 12,000-

287   year period (Table 1): 16 samples are anthropogenic dates from the site Cueva Huenul 1 located in

288   the same rocky outcrop (Barberena, 2015) where the middens were collected, and the remaining 16

289   samples were obtained from the rodent middens. Figure 3 juxtaposes the summed probability

290   distributions of these dates classes. The blocks of pale red and blue show the five modeled phases

291   of alternating human – rodent occupation, under the best model. The maximum likelihood parameter

292   estimates for the phase transition dates in model 4 (Table 2) suggest three human occupancy phases

293   at Huenul: firstly, between 12,000 to 10,339 cal yr BP (archaeological component 1), secondly a

294   very short phase between 5553 to 5472 cal yr BP (component 3), and thirdly a phase between 1704

295   to 300 cal yr BP (component 4). Additionally, we have also recorded a paleontological component

296   1 dated to the late Pleistocene (16,695 to 13,631 cal yr BP), for which no human occupations were

297   recorded (see detailed contextual information in Barberena, 2015; Barberena et al., 2015b).

298   When comparing the dates for rodent middens and human occupations, our results show

299   that model 4 best fits the data (lowest BIC, Table 2), and the Bayes Factor shows this is over 9

300   million times more likely than model 0, allowing us to reject the hypothesis that humans and rodents

301   coexisted throughout the 12,000-year period, and instead favoring the most likely model that their

302   respective occupancies were mutually exclusive in alternating discrete phases. This finding indicates

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303 a lack of occupational superimposition on the local scale of the rocky outcrop of the Huenul locality,

304 not necessarily implying that this is a regional pattern. Models 1, 2 and 3, on the other hand, perform

305 badly and are substantially poorer than the null hypothesis. From model 4 onwards, the maximum

306 likelihood is higher than for the null model and continues to improve with each additional parameter.

307 However, the lack of improvement in the BIC after model 4 shows that this increasing complexity

308 is not justified and results in over fitting.

309
310 *4.2 Agents of midden-formation: A paleoparasitological assessment*

311 A total of 21 of the 60 fecal samples contained parasites. The eggs of parasites found were

312 assigned to *Heteroxynema* (Cavioxyura) viscaciae Sutton and Hugot, 1989 and *Helminthoxys* sp.

313 (Nematoda: Oxyuridae), *Trichuris* sp. (Nematoda: Trichuridae), and one unidentified nematode.

314 Based on the rodent species present in the study area (Fernández et al., 2015; Pardiñas and D'Elía,

315 2015), the aspect of fossil rodent middens and of the coprolites examined (Fig. 2c), the eggs of the

316 parasites found, and the knowledge of the parasitic fauna of vizcachas, the feces were attributed to

317 the mountain vizcacha *Lagidium viscacia* (Caviomorph: Chinchillidae; Fig. 2d). Mountain

318 vizcachas are large caviomorph rodents that inhabit arid regions of western and southern South

319 America, from the highlands of Ecuador through the Andes of Peru and Bolivia to the coastal

320 mountains of Chile and Patagonian steppe of Argentina. This rodent is found in rocky outcrops and

321 is highly gregarious, living in colonies that may range widely in size (Spotorno and Patton, 2015).

322 The biological cycle of parasites found were discussed in detail in Beltrame et al. (2016).

323
324 *4.3 Plant macrofossil record*
325
326 A total of 30 plant macrofossil taxa were identified for all samples, 13 of which were

327 identified to the species taxonomic level and 17 to genus level (Fig. 4, Fig. 5; Table 3).

328 For samples with ages between 10,400-9400 cal yr BP, a total of 23 taxa were recorded.

329 These samples are dominated (Relative Abundance Index: 3=dominant) by Monte taxa such as

330 *Prosopis* sp. associated with *Acantholippia seriphioides* and elements of Patagonia (*Baccharis* sp.,

331 *Adesmia* sp., *Berberis* spp., *Junellia seriphioides*, *Balbisia gracilis*, *Lupinus* aff. oreophilus,

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332 *Nassauvia axilaris*). Taxa such as *Schinus* sp. and *Ephedra* sp., characteristic of the Monte-

333 Patagonia transition, are rare (RAI: 1=rare), while the presence of cacti (*Maihuenia patagonica*)

334 are recorded as frequent (RAI: 2=common). Among the grasses, *Poa* sp. and *Hordeum* sp. are

335 dominant (RAI=3) while *Festuca* sp., *Bromus* sp. and *Jarava* sp. rare (RAI=1).

336   For samples with ages of 9200, 6500 and 5700-5500 cal yr BP, the richness and diversity

337 of species is the lowest for the whole record. Assemblages of plant macrofossils are dominated

338 Monte taxa (RAI= 2 or 3) represented by *Prosopis* spp., *Larrea* sp., *Acantholippia seriphioides*

339 except for the 5700 cal yr BP assemblage, which presents low abundance of Patagonia elements

340 (*Baccharis*, *Junellia seriphioides*, and *Hordeum*). Those assemblages dominated by Monte taxa are

341 associated to Monte-Patagonia transition taxa including *Schinus* sp., *Ephedra* sp. and

342 *Hoffmannseggia* sp. which are rare (RAI=1) while Patagonian taxa (RAI= 1 or 2) includes shrubs

343 (*Baccharis* sp., *Adesmia cf. offcinalis*, *Lupinus aff. Oreophilus*), dwarf shrubs (*Euphorbia* sp.,

344 *Perezia aff recurvata* and *Nassauvia axilaris*), and grasses (*Festuca* sp., *Jarava* sp., and *Poa* sp.).

345 are present. The cacti *Maihuenia patagonica* is also present at 6500 cal yr BP.

346   *Prosopis* sp. dominates (RAI= 2 or 3) along with other Monte taxa such as *Larrea* sp. and

347 *Acantholippia seriphioides* (RAI= 1) between 4200-3800 cal yr BP in association with Monte-

348 Patagonia elements including *Schinus* sp., *Ephedra* sp., and *Senecio* sp., as well as Patagonian

349 elements (*Berberis* spp., *Junellia seriphioides*, *Gilia crassifolia*, *Mulinum spinosum*, *Nassauvia*

350 *axillaris*, among others).

351   For samples with ages between 3500 and 2500 cal yr BP, the macrofossil assemblages are

352 co-dominated by Monte elements (*Prosopis* sp. RAI: 3=dominant), Monte-Patagonia transition

353 elements such as *Schinus* sp. and *Ephedra* sp. (RAI <2) and Patagonian (RAI <2) including shrubs

354 such as *Berberis* spp., *Junellia seriphioides*, *Mulinum spinosum*, *Nassauvia axilaris* and grasses

355 (*Festuca* sp., *Jarava* sp. and *Poa* sp.).

356

357 *4.4 Pollen record*

358   The pollen record of the Huenul rodent midden series comprises a total of 30 pollen types

359   (Fig. 6) and is divided in two zones and two subzones (Fig. 7):

360   **Zone HU1a** (10,400-9400 cal yr BP) is dominated by *Larrea* (50-15%) associated with

361   *Prosopis* (25-5%), Solanaceae (*Lycium* type; 10%), *Schinus* (20-5%), *Ephedra* (25-5%) and

362   Poaceae (15-5%). Ast subf Ast (*Senecio* type), Fabaceae (*Adesmia* type), Ast sub Ast (*Baccharis*

363   type) and Ast subf Mut (*Chuquiraga*) are present in percentages under 12%. Amaranthaceae, an

364   azonal pollen type (and therefore excluded from the basic pollen sum) growing in the perennial

365   stream in Huenul locality.

366   **Zone HU1b** (9200, 6500 and 5700-5500 cal yr BP) is dominated by *Larrea* (60-25%) along

367   with Prosopis (<20%), Solanaceae (*Lycium* type; <20%), *Schinus* (<10%) and Poaceae (20-5%).

368   Other Monte or Patagonia pollen types are present in percentages under 10%, whereas

369   Amaranthaceae values ranges between 35-20%.

370   **Zone HU2a** (4200-3800 cal yr BP) is co-dominated by *Larrea* (<20%), *Ephedra* (40-10%),

371   Ast subf Ast (*Senecio* type), Poaceae (25-20%) along with *Schinus*, Ast subf Ast (*Baccharis* type),

372   Fabaceae (*Adesmia* type), Ast subf Mut (*Chuquiraga* and *Proustia, Nassauvia* types) and Apiaceae

373   (*Mulinum* type) with values under 15%. Amaranthaceae values remains under 25%.

374   **Zone HU2b** (3500 and 2500 cal yr BP) is a subzone integrated by two pollen assemblages

375   quite different to each other. The older one dominated by *Larrea* (45%) along with Solanaceae

376   (*Lycium* type; 15%) and Poaceae, whereas the younger one is co-dominated by *Larrea* (10%),

377   *Ephedra* (20%), Ast subf Ast (*Senecio* type; 15%) and *Poaceae* (20%). Amaranthaceae values are

378   under 20%.

379

380   *4.5 Summed Probability Distribution analysis of the[14]C database*

381

382   The overall anthropogenic database comprises 580 ^{14}C dates from 244 sites. We constrain

383   our study period to 12,000 to 2,500 cal yr BP, which encompasses 573 calibrated dates from 240

384   sites. Figure 8 shows the Summed Probability Distribution (SPD) of this database, which conforms

385   extremely well to a fitted exponential model of steady background population growth and

386   taphonomic loss. Although there are a few sections of the SPD that sit outside the null 95% CI

387   ribbon, these are few, sporadic, and the size of their deviation is only marginally outside the ribbon.

388   As such, these are to be expected given that approximately 5% of any random simulation can be

389   expected to sit outside the ribbon, and therefore can be considered false positives. Indeed, the p-

390   value of 0.4265 means that we cannot reject the null hypothesis.

391

5. Discussion

392
393
394
395   *5.1* Lagidium *as a midden-forming agent*
396
397   On the basis of the aspect of fossil rodent middens, the characteristics of the coprolites

398   examined, the knowledge on the parasitic fauna of vizcachas, and the eggs of the parasites found

399   (*Heteroxynema* [Cavioxyura] viscaciae and *Helminthoxys* sp. [Nematoda: Oxyuridae]), the feces

400   were attributed to the mountain vizcacha *Lagidium viscacia* (locally known as chinchillón or

401   vizcacha), which we assigned as the only producer of the Huenul series midden record. Indeed,

402   *Lagidium* is one of the main midden-producers throughout semi-arid and arid South America

403   (Betancourt and Saavedra, 2002). It is a syntopic rodent of medium size (ca. 2000 g) that belongs

404   to the Chinchillidae family (Redford and Eisenberg, 1992). In Argentina it inhabits exclusively

405   rocky environments with scarce vegetation cover, either in the high peaks of the Andes even above

406   3000 masl, or in the isolated canyons and fences of extra-Andean Patagonia. The vizcachas are an

407   herbivore-rodents with morning and crepuscular habits and a foraging range that is concentrated

408   within 30 m from the rocky outcrops that it occupies, where they live in family groups (Walker et

409   al., 2000). The restricted foraging activity of the vizcacha suggests that the macrofossil botanical

410   record from the middens is a proxy of the vegetation cover in the immediate surroundings of the

411   middens. In terms of diet, the vizcacha has a specialized feeding behavior despite its consumption

412   of a wide variety of plant species (Galende et al., 1998; Galende and Raffaele, 2012). However,

413   this feeding behavior was particularly observed in grass-dominated environments, while no similar

414 surveys are available for vizcachas living into shrub dominated landscapes like the Monte around

415 Huenul locality.

416

417 *5.2 Pollen vs. plant macrofossils record*
418

419 The pollen and plant macrofossil records show similar environmental changes in time and

420 direction, but there are differences related to the spatial scales represented by these proxies and by

421 their taphonomy. Thus, the pollen record reflects changes of greater magnitude than the macrofossil

422 record. However, changes in abundance and diversity in the macrofossil record complement at a

423 local scale the regional trends of vegetation changes informed by the pollen record.

424 While pollen of azonal (Amaranthaceae) and long distance plants (*Nothofagus*) are present

425 in the midden pollen assemblages, they are poorly represented or completely absent in the

426 macrofossil record, respectively, due to the pollination syndrome of species within those

427 family/genera and the different spatial scales represented by the pollen (local/regional) and plant

428 macrofossil (local) records. On the other hand, plant macrofossil assemblages show a clear decrease

429 in diversity during the mid-Holocene that is not reflected as clearly in the pollen record, which only

430 shows a decrease in pollen percentages of many Monte-Patagonia transition and Patagonia pollen

431 types. Similar issues were described and discussed earlier regarding pollen and macrofossil records

432 preserved in rodent middens from the Atacama Desert, located northwards in the SAAD

433 (Maldonado et al., 2005; de Porras et al., 2017).

434

435 *5.3 Environmental reconstruction*

436 Plant macrofossil and pollen records from the Huenul midden series synchronously reflect

437 the occurrence of moderate environmental and vegetation changes in the Monte-Patagonia ecotone

438 at 36°S since the early Holocene (Figs. 5, 7).

439 During the early Holocene (10,500- 9400 cal yr BP), Monte-like vegetation dominated by

440 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 seasonal climate regarding the precipitation regime.

An intensification of dry conditions is evident around 9.2ka 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 9400-9200 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 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

16

467   the previous period, while *Nothofagus dombeyi*-type, originated in the forests along the Andes,

468   increased up to 15%, probably indicating an enhanced W-E pollen transport by surface winds

469   related to the Southern Westerlies. Similar but more moderate humidity conditions prevailed during

470   the late Holocene (3500-2500 cal yr BP), as indicated by an increase of percentages of Monte-

471   Patagonia transition elements.

472   Macrofossil assemblages are co-dominated by Monte, Monte-Patagonia and Patagonia

473   elements, suggesting an amelioration of moisture conditions in two distinct phases. Between 4200-

474   3800 cal yr BP, the abundance of *Mulinum spinosum* and most of the grasses along with an increase

475   in diversity indicate the most humid period of the Holocene, coinciding with the pollen record.

476   Between 3500-2500 cal yr BP, the co-dominance of elements belonging to the three vegetation

477   units along with a reduction of diversity and, particularly, the abundances of grasses, reveal slightly

478   wetter conditions than present, but drier than the precedent period. In synthesis, both records reflect

479   increased humidity at the local and regional scales during the late Holocene, which would result

480   from an increase in winter precipitation due to a higher incidence of the Southern Westerlies.

481

482   *5.4 Regional paleoclimatic integration*

483   On a regional scale, the records from the lee side of the Andes [Mallín Vaca Lauquen

484   (MVL), 36.5°S, Markgraf et al., 2008; Laguna El Trébol (LET), 41°S, Whitlock et al., 2006] showed

485   cold and dry conditions during the late Glacial (17,000-15,000 cal yr BP) followed by a gradual

486   increase of temperature but still under drier conditions than present, which lasted up to the

487   Pleistocene-Holocene transition (15,000-11,500 cal yr BP; Fig. 9). While these conditions prevailed

488   in MVL, the record from LET suggests drier conditions during the early Holocene (11,500-8000 cal

489   yr BP) and the beginning of the mid-Holocene (8000-6000 cal yr BP), associated to an increased

490   frequency of crown fires. Eastwards from these sites, the Huenul rodent midden series (HU) supports

491   this latter climatic scenario reflecting drier than present conditions under a marked seasonal

492   precipitation regime between 10,500-9400 cal yr BP (Fig. 9). Therefore, records from northern

493   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).

520   The late Holocene was characterized by highly variable climatic conditions across northern

521   Patagonia, which remained relatively similar to those described after 6000 cal yr BP for the

522   southernmost area (>36°S; Fig. 9). The northernmost (<35°S) records, on the other hand, reflected

523   Neoglacial advances between 6400 and 4800 cal yr BP (RV, 35°S; Espizúa, 2005; Espizúa and

524   Pitte, 2009) coinciding with the most humid conditions at HU area around 4500 cal yr BP, followed

525   by a reduction of humidity between 3500 and 2500 cal yr BP (Fig. 9). In contrast, the pollen record

526   of LES (35°S; Navarro et al., 2012) shows a change towards moderately drier conditions up to the

527   present (Fig. 9). Widespread wetter conditions during the late Holocene may be attributable to

528   intensified westerly flow since 6000 BP at the centennial-millennial scales associated to the onset

529   of El Niño-like inter-annual variability (Whitlock et al., 2006; Abarzúa and Moreno, 2008; Iglesias

530   et al., 2011).

531

532   5.5 *Climate change and human occupations in the SAAD*

533   The diachronic analysis of anthropogenic radiocarbon dates from the central-western area

534   of the SAAD at 36°S conforms to a fitted exponential model of steady background population

535   growth and taphonomic loss, not suggesting significant demographic changes that may have been

536   the result of the impact of climate change. Given the size of our database and the power of the

537   methods used, and against previous interpretations (Barberena et al., 2017), we cannot attribute the

538   fluctuations in the observed SPD to demographic events (see also Perez et al., 2016; Gordón et al.,

539   2019), which may instead represent artifacts of small sample size and/or calibration. Significantly,

540   this includes the mid-Holocene, for which there is considerable debate regarding the existence of

541   archaeological hiatuses or troughs (Gil et al., 2005; Neme and Gil, 2009; García, 2010; Méndez et

542   al., 2015; Durán et al., 2016; Barberena et al., 2017). The local paleoecological results and macro-

543   regional synthesis presented here simultaneously signal that the most arid conditions took place

544   during the mid-Holocene. While the effect of small sample size of the radiocarbon database cannot

545   be yet discarded, it is not possible to tie this dry period to significant demographic shifts in this

19

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 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 (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 case 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.

Acknowledgements

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FIGURE CAPTIONS

822

823 Figure 1. (a) Annual precipitation map of southern South America (Fick and Hijmans, 2017)
824 showing the South America Arid Diagonal (SAAD) as the area under 400 mm of annual
825 precipitation, location of the study area and sites mentioned in the text; (b) climograph for Buta
826 Ranquil, a town located 10 km southwards Huenul locality and; (c) regional vegetation map based
827 on Oyarzabal et al. (2018) including sites mentioned in the text. Base map was plotted using QGIS
828 3.12. applying the ESRI World Hillshade.

829

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

833

834 Figure 3. Summed Probability Distributions (SPD) of calibrated radiocarbon dates from human
835 occupations (red) at Cueva Huenul 1 and rodent middens (blue) from Huenul locality. Note that the
836 rodent middens SPD y-axis is inverted to aid the comparison with human occupations SPD.

837

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

844

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

849

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

855

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

859

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

863

864 Figure 9. Schematic comparison of midden data from the Huenul series (coloured circles) and the
865 summed probability distribution (SPD) of the anthropogenic ^{14}C database at the regional scale with
866 palaeoclimatic conditions inferred from previous surveys in northern Patagonia (Argentina)
867 including Holocene glacial advances in Río Valenzuela (Espizúa, 2005; Espizúa and Pitte, 2009);

868   the pollen record of Laguna El Sosneado (Navarro *et al.*, 2012) and the pollen and charcoal records

869   of Mallín Vaca Lauquen (Markgraf *et al.*, 2008) and Laguna El Trébol (Whitlock et al., 2006)].

870

871   TABLE CAPTIONS

872

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

874   locality

875

876   Table 2. Summary of the seven models utilized in the phase model comparison of the timing of

877   human occupations and rodent middens in the Huenul Locality. Model 4 (phases of human – rodent

878   – human – rodent – human occupancy) has the lowest value for the Bayesian Information Criterion

879   -BIC, indicated in bold- (parameter date estimates are aligned to show similarities between models).

880

881   Table 3. List of plant species identified in the rodent midden macrofossil record of Huenul locality.

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