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New palaeoecological approaches to interpret climatic fluctuations in Holocenic sites of the Pampean Region of Argentina

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Abstract

The apparently regular and favourable climate that characterizes the Holocene as an interglacial period shows, however, important climatic instability well documented in the Northern Hemisphere. These fluctuations from colder to warmer or wetter to drier affected both biodiversity and human societies in the last 12,000 years, although the impact in Southern America is still poorly known. We are here investigating the biodiversity of small mammal faunas, more sensitive to climatic changes than large mammals, combining taphonomic and palaeoecological data in the Argentine Pampas to better understand the global nature and effect of these Holocene climatic fluctuations. This paper is pioneering applying in this region palaeoecological methodologies practised in European sites, such as the chorotype classification and biomes overlap analyses. The Pampean Region is an ecotone with a confluence of three climatic regions where any change in climatic conditions should be easily detected. Our results, based on the palaeoecological requirements of small mammals, do not indicate severe changes, and most of the sites show climatic stability except for one of them, in which a possible trend towards present conditions (temperate/humid) can be inferred.

Keywords: Climatic change Aridity Temperature Central-east Argentina Chorotypes

Introduction

One of the principal sources of palaeoecological information in both archaeological and palaeontological sites are small mammal faunas. The reason of considering small mammals to infer past ecological conditions lies in: i) they make up a large proportion of some fossil mammal assemblages, often being both abundant and taxonomically diverse (e.g. Andrews, 1990; Pardinas, 1999a); ii) they are usually highly dependent on the vegetation cover; iii) most of the species have relatively narrow environmental requirements, being frequently associated to particular habitats; iv) due to their physiology and lifestyle, they are more strongly correlated with climatic variables (e.g. annual precipitation and temperature) than large mammals (Andrews, 1995; Andrews and O'Brien, 2000, 2010). This close relationship of small mammals with their surrounding environment allows the possibility to detect even short climatic events. Therefore, small mammal faunas can aid in the recognition of climatic variations during the Holocene, a period characterized by climatic changes at global and regional scales (see Mayewski et al., 2004 and reference therein). The short climatic events of the Holocene may have involved very fast faunistic replacements, mixing allopatric species (species whose distribution areas do not overlap) (Pardinas and Teta, 2000) and producing small mammal faunal assemblages with no present counterpart (Pardinas, 1999a; Pardinas and Teta, 2000; Goin, 2001; Quintana, 2001a). In this sense, the Pampean Region (central-east Argentina) has demonstrated to be especially sensible for the detection of rapid faunal replacements (see Pardinas, 1999a; Pardinas and Teta, 2000; Goin, 2001; Quintana, 2001a; Tonni, 2017). The location of the Pampean Region in an ecotone between arid (Patagonian) and humid (Brazilian) zones favours the entrance of small mammal species from these areas during climate changes, which results in an ideal place to evaluate palaeoclimatic, palaeoenvironmental and palaeoecological patterns (Quattrocchio et al., 2008; Tonni, 2017). In fact, the record of short global climatic events, well known in the Northern Hemisphere, such as the Medieval Climatic Anomaly (MCA) and the Little Ice Age (LIA), has been apparently identified in the Pampean region based on some small mammal assemblages (e.g. Pardinas, 1999a; Tonni, 2017). Apart from MCA and LIA, other cooler events have been suggested to have large impact on Northern Hemisphere, like the 8.2 ka and 4.2 ka events (e.g. Bond et al., 1997). They have been recorded in several proxies, such as archaeological records, speleothems, lacustrine settings or pollen data, in Western Europe (e.g. García-Martínez de Lagran et al., 2016; Straus, 2018; Bini et al., 2019; Di Rita and Magri, 2019). The 8.2 ka and 4.2 ka events may have also involved very fast replacements or abundance changes in the composition of small mammal fauna fossil assemblages. In the Iberian Peninsula, a cool, arid phase has been suggested in the MIR4 level from El Mirador cave (Atapuerca, Burgos), associated to a high percentage of the arvicoline rodent *Microtus arvalis*, a Eurosiberian taxon linked to open dry environments (Banuls-Cardona et al., 2017). This phase has been recorded between 4330 and 3070 cal yr BP, coinciding with a global dry pulse associated to the effects of the 4.2 ka Bond event between 4200 and 3800 cal yr BP (Mayewski et al., 2004). However, the consequences of these events in the Southern Hemisphere are poorly known. For the 8.2 ka event, some records, based on speleothems from Brazil, seem to indicate wetter conditions within the South America monsoon system region (e.g. Cheng et al., 2009; Stríkis et al., 2011; Bernal et al., 2016). On the other hand, dry conditions are known through a fall in the lake level of Mar Chiquita (Argentina) at ca. 8.2 ka and between 5 and 3 ka (Piovano et al., 2009; Forman et al., 2014). Prominent aridity is also inferred from the San Luis dune field (western Argentina), where high angle-cross beds of a large longitudinal dune filled a drainage at ca. 4.2 ka (Tripaldi and Forman, 2007; Forman et al., 2014).

Despite small mammals are considered good climate indicators, their presence in fossil sites is influenced by the predatory activity and predator preferences (Andrews, 1990). In these cases, taphonomic analyses performed on the small mammal assemblages are necessary to recognise the predator and to infer the ecosystem occupied by prey and predators, as well as to confirm whether certain inferred climatic changes are truly indicated by the prey or are just a consequence of hunting habitat preferences of the involved predator.

In the Pampean Region, one of the potential predators of the so-called 'small game' (Stiner et al., 2000) are humans. Abundant ethnographic references (e.g. Gusinde, 1951; 1982; Bridges, 1952; Aguerre, 2000; Popper, 2003) confirm the easy capture by humans of fossorial micro- and mesomamammals that live in colonies. These animals might be caught or trapped as a daily source of food along with other nutritional sources from gathering nuts, roots, plants, eggs or insects, plus hunting large mammals.

Apart from predatory activity, the presence of different taphosystems in the area needs to be considered. Mainly two theoretical taphosystems are recognized in the region: open-air sites and rockshelters. The term taphosystem is proposed and defined by Fernandez-Lopez (1984) as the combination of a preserved fossil association and its outer environment (before and after burial). The concept of taphosystem allows us to better characterize general vs. particular taphonomic traits of each site with respect to production and preservation modes, potential mixtures and diagenetic processes, in order to distinguish preservation modes from key palaeoecological traits.

Therefore, the main aim of this work is to revise the Holocene small mammal faunas in the Pampean Region to understand regional climatic and environmental variability, focused on five archaeological sites. Our review also intends to evaluate if the Holocene events, well defined in the Northern Hemisphere, can be confidently recognized, and characterized in the Pampean Region. The selected archaeological sites also allow us to evaluate the respective taphonomic histories and how human activities in the past may affect palaeoenvironmental reconstructions. The used methodologies have been extensively applied in Western Europe and demonstrated to be a useful tool to obtain detailed palaeoecological data (e.g. Evans et al., 1981; Blain et al., 2009; 2016; Lopez-García et al., 2010; Andrews et al., 2016; Banuls-Cardona and Lopez-García, 2016; Banuls-Cardona et al., 2017).

Study area

The Pampean Region occupies a large area (370.000 km^2), located at the central-east part of

Argentina. The predominant climate is temperate, determined by the Atlantic anticyclone, which decreases its influence from the northeast (mean annual precipitation of 1200 mm; mean annual temperature of 18 °C) to the southwest (mean annual precipitation of 600 mm; mean annual temperature of 14 °C; Burgos, 1968). Thus, the Pampean Region (Fig. 1) is traditionally divided into the Humid Pampa towards the northeast and the Dry Pampa towards the southwest (Mancini et al., 2005; Prado et al., 2015) and three different ecoregions are recognized: Pampa (corresponding to the Humid Pampa), Espinal and Low Monte (both associated to the Dry Pampa) (Burkat et al., 1999; Mancini et al., 2005). The predominant vegetation of the Humid Pampa is characterized by grasslands (dominated by Poaceae), with some marginal xeromorphic forests (mostly of *Celtis tala*) along the coast. This vegetation is gradually transformed into arid steppes dominated by more xeric plants of the Dry Pampa (Oyarzabal et al., 2018). The selected archaeological sites are located in the Humid Pampa (Fig. 1, Table 1) in an area susceptible to climate fluctuations linked to arid conditions due to its proximity to the Dry Pampa; in fact, Mancini et al. (2005) indicated an eastward shift of the Dry Pampa limit between 8000 and 4000 yr BP. This displacement is also linked to the Holocene marine transgression, which affected the littoral communities of the Pampa grasslands (Isla, 1989, 1998).

The small mammal fossil assemblages from the Pampean Region have been intensively studied from taxonomical, stratigraphic and phylogenetic perspectives (e.g. Pardinas, 1999a; 1999b; D'Elía et al., 2005; Fernandez et al., 2012; Teta, 2017). Most of the modern small mammal taxa of the Pampean Region have been present since the Late Pleistocene (e.g. Pardinas et al., 2010, and references therein). Extant taxa such as the sigmodontine rodents Calomys (*C. musculinus* and *C. laucha*), *Oligoryzomys flavescens, Akodon azarae, Reithrodon auritus, Eligmodontia typus, Oxymycterus rufus, Holochilus vulpinus, Scapteromys aquaticus, Necromys lasiurus* and *Graomys griseoflavus* have undergone changes in their abundances and have occupied different geographic areas (e.g. Pardinas et al., 2010, and references therein). Most of the small mammal assemblages from the Last Glacial Maximum (LGM, ca. 23e18 ka) were dominated by a mixture of sigmodontine rodents linked to temperate grasslands, such as *R. auritus* and *A. azarae*, and other inhabitants of shrubby arid and semiarid environments, such as *E. typus* and *G. griseoflavus*.

The latter two became locally extinct in a large extension of the Pampean Region during postglacial times, from ca. 13 ka to the Early Holocene (Pardinas and Teta, 2010). Some archaeological sites show the presence of small mammal fauna assemblages without a present counterpart during the Early Holocene. In the central-east Humid Pampa, species linked to arid conditions, such as the mustelid *Lyncodon patagonicus*, the caviid rodent *Microcavia australis*, the marsupial *Lestodelphys halli*, and the armadillo *Tolypeutes matacus*, are found together with subtropical rodents (e.g. *H. vulpinus* and *S. aquaticus*) that suggest higher temperatures and precipitations. This mixture probably indicates the presence of relict populations, although an arid pulse after post-glacial amelioration has also been suggested (Pardinas 1999a, 1999b; Tonni et al., 1999; Prevosti and Pardinas, 2001; Scheifler et al., 2015).

During the Middle Holocene, the incidence of humid and warmer conditions is inferred from the presence of *H. vulpinus* and *Monodelphis dimidiata* around 6.5e6 ka (Crivelli Montero et al., 1997), corresponding to the Holocene Climate Optimum (HCO, ca. 7.5e6 ka) (Pardinas, 1999b). At the end of the Middle Holocene (4.7 ka), the presence of the caviomorph *Microcavia* cf. *M. australis* suggests a change towards more arid conditions (Tonni and Cione, 1984; Pardinas, 1999a, 1999b; Soibelzon and Leon, 2017).

The Late Holocene has yielded small mammal assemblages with several extant rodent species such as *Cavia aperea*, *R. auritus*, *O. flavescens*, *A. azarae*, *Calomys* spp. and *N. lasiurus*, and others out of their current geographic distribution. The warmer temperatures of the MCA (Lüning et al., 2019) could have favoured the arrival of the subtropical and Chacoan sigmodontines *Pseudoryzomys simplex* and *Bibimys torresi* (e.g. Pardinas et al., 2010, and references therein), in the area, two species with restricted distributions today: *P. simplex* is not found in the Pampean Region nowadays, and *B. torresi* only inhabits a small area at the north of Buenos Aires Province. *Pseudoryzomys simplex* and *B. torresi* were probably common elements of the Chaco and Pampean Regions through the Late Holocene, but underwent a severe retraction to the north in the last two centuries, due to the negative effects of intensive agriculture and the presence of livestock (e.g. Scheifler et al., 2012; Teta et al., 2014; Pardinas et al., 2017). On the other hand, this anthropic context has favoured the presence of the opportunistic sigmodontines *Calomys* spp., *A. azarae* and *O. flavescens*, which dominate in the modern communities (e.g. Pardinas et al., 2010; Fernandez et al., 2012). Finally, during the LIA, the sigmodontines *E. typus* and *Phyllotis* sp. took advantage of the arid conditions to get into the Pampean Region from Patagonia, possibly using the coastal dunes as a corridor (Pardinas, 1999b; Pardinas et al., 2010).

Material and methods

Archaeological sites

The five Holocene localities with small mammal assemblages (Table 1) from central-east Argentina (Fig. 1) analysed in this paper have been systematically excavated and have extensive taxonomic, taphonomic, stratigraphic, sedimentological and chronological information. Some of the sites include Late Pleistocene levels that are also included in this study to provide more complete sequences. The sites correspond to open-air and rockshelter taphosystems.

We analysed the taphonomic and palaeoecological data obtained after an exhaustive bibliographic review, which has been used as the basic source for taxonomic identification, chronology, and taphonomic analyses (see references for each site in Tables 1-3, respectively). A description of each site is included below, and their respective dates are presented in Table 2. Table 3 shows information about the main predators identified as the principal agents for the accumulation of small mammals at each site (see Supplementary Material for detailed information on the taphonomic traits). Most of the small mammal assemblages were originally described as accumulations produced by Tyto alba, which has been recently taxonomically renamed in South America as Tyto furcata (e.g. Aliabadian et al., 2016; Enriquez et al., 2017). This new nomenclature was applied for this work.

The application of systematic archaeological excavations provided detailed descriptions for the sedimentological sequences of the analysed sites. All this suggests that dating obtained from each site should be considered reliable and correlations with the Holocene events proposed in Table 2 are, therefore, reasonably confident. The events were proposed following the time intervals indicated by

Mayewski et al. (2004) for the 8.2 (9000 to 8000 cal yr BP) and 4.2 (4200 to 3800 cal yr BP) ka events. Dates exceeding the end of these events were also considered to corroborate a possible delay in the response of small mammal faunas. This delay was initially suggested by Alberdi et al. (1995) for the faunas of the Southern Hemisphere respect to the Northern Hemisphere during the last 5 million years.

Laguna Cabeza de Buey 2 (LCB2)

Laguna Cabeza de Buey 2 is an open-air archaeological site located in the west area of the Humid Pampa (Politis and Barros, 2006; Fig. 1c). The site is placed at the shore of a semipermanent shallow lake in the Vallimanca Basin, where other temporal and permanent lakes are present (Messineo and Scheifler, 2016). Excavations since 2011 revealed five major stratigraphic units (from base to top U-V, U-IV, U-III, U-II and U-I), covering a chronological sequence from the Late Pleistocene to the Late Holocene (Messineo et al., 2019). All the units show the presence of fine sands, indicating that sedimentation was dominated by aeolian processes associated to parabolic dunes and aeolian sand sheets in the interdune areas, affected by post-depositional processes, including bioturbation by roots, insects, and animals (Messineo and Pal, 2019; Messineo et al., 2019).

Amongst the archaeological materials recovered from Laguna Cabeza de Buey 2, diverse cultural elements (i.e. lithics, pigments, charcoals or pottery fragments), together with bone and teeth fragments from extant and extinct species, were found (Messineo and Scheifler, 2016). The lower unit (U-V) is culturally sterile (Scheifler and Messineo, 2016; Messineo and Pal, 2019; Messineo et al., 2019).

Cueva El Abra (CA)

The rockshelter archaeological site of Cueva El Abra is located in La Vigilancia mountain range, at the eastern part of the Tandilia hilly system (Mazzanti and Bonnat, 2013; Quintana, 2016a; Fig. 1c). Four allostratigraphic units are recognized in the site with a fining upward sequence (sandy-clay silts to clay-sandy silts) (Martínez and Mazzanti, 2017) and they are divided in Lower (U4 and U3) and Upper (U2 and U1) archaeological components. The sequence covers two different temporal lapses: Late Pleistocene-Early Holocene (U4 and U3) and Late Holocene (U2 and U1) (Mazzanti et al., 2012; Quintana, 2016a; Martínez and Mazzanti, 2017).

The archaeological sequence indicates an intense use of the site by the hunter-gatherer groups in several times, especially during the Late Pleistocene and Early Holocene (Mazzanti et al., 2012; Quintana, 2004). Archaeological material has been recovered from both components, but the Upper component shows a greater abundance of microvertebrate remains (Quintana et al., 2003; Quintana and Mazzanti, 2011; Quintana, 2015).

Cueva Tixi (CT)

Located in La Vigilancia mountain range, in the Tandilia hilly system (Fig. 1c), Cueva Tixi is considered an archaeopalaeontological rockshelter site (Quintana, 2016b). The stratigraphic sequence is divided in six units (F, E, D, C, B and A) (Figini et al., 1985; Mazzanti, 1993). Unit A is characterized by a calcium carbonate layer and the absence of faunal and cultural remains (Martínez and Osterrieth, 2001; Mazzanti and Quintana, 2002). The remaining units show a finning upward sequence from sandy-silts to clay-silts. The Unit was subdivided in Lower and Upper subunits due to chronological, archaeological and faunistic differences (Mazzanti, 2001; Quintana, 2001a). The stratigraphic sequence covers a wide temporal interval from the Late Pleistocene to the Late Holocene (Quintana and Mazzanti, 2001, 2010, 2011). Faunal remains mainly come from units E, C, D and B, and constitute a referent of the vertebrate diversity from the Tandilia hilly system (Quintana, 2001a, 2016b).

Paso Otero 4 (PO4)

The open-air site of Paso Otero 4 is in the middle stream of the Quequen Grande River, in the Paso Otero archaeological locality (Fig. 1c). This river probably flowed near or through the Paso Otero locality due to a small shift in the watercourse during the Early and Middle Holocene. The site mainly consists of fine diatomaceous sediments and was formed by calmed depositional processes (Martínez and Gutierrez, 2019).

Paso Otero 4 was divided into Upper and Lower levels, based on the recovered extinct fauna. Several zooarchaeological materials were found, amongst them: eggshells, armadillo osteoderms and skeletal elements from large and small mammals, birds, amphibians and reptiles (Martínez et al., 2013; Alvarez et al., 2013). Lithic materials were also recovered, including tools, cores, lithic debris and ecofacts (Barros, 2012).

Arroyo Seco 2 (AS2)

Arroyo Seco 2 is an open-air archaeological site which is located at the southeastern part of the Buenos Aires province. This site records extinct Pleistocene megafauna, anthropic remains and human burials (e.g. Fidalgo et al., 1986; Politis et al., 1987; 1988; 1992; 1995; Politis and Salemme, 1989; Politis and Beukens, 1991). Faunal remains suggest several occupational events and provide information about the activities of the hunther-gatherer societies from the Late Pleistocene to the Late Holocene (Politis et al., 1995). The stratigraphy of Arroyo Seco 2 is complex, with a total of five stratigraphic units (from base to top: ‘Z’, ‘S’, ‘Y’ and ‘X’) and two possible unconformities, one at the base of the Unit S and another at the base of the Unit X (Fidalgo et al., 1986). Intrusive human burials were found in the Unit Z (see Politis et al., 2016). Abundant lithic and faunal remains from extant and extinct species come from all units, except for Unit Z, in which the scarce bone fragments recovered mainly belong to rodents. Megafaunal remains were recorded from unit Y, where a concentration of distal limb bones of *Megatherium americanum* was found (Politis et al., 2016 and references therein).

Palaeoecological analyses

Palaeoecological analyses haven been performed through a new ecological approach for the study area based on previous methods typically used in Western Europe. These analyses combined: 1) Diversity indexes and body mass classification; 2) an ecoregion overlap analysis, based on the Mutual Ecographic Range (MER) method (Blain et al., 2009, 2016), using presence/absence data; 3) the Habitat Weighting method (e.g. Evans et al., 1981; Andrews et al., 2016) and 4), a chorological classification (e.g. Marquez et al., 1997; Sans-Fuentes and Ventura, 2000). All of them are applied for the first time to Argentinian assemblages, the last two methods based on abundance data.

Body mass classification

Body mass classification allows the possibility to compare whether the distribution of category sizes varies between the taphosystems, due to the different preservation environments, or the presence of certain predators is also favouring the accumulation of some categories.

Small mammal faunas herein considered include species classified as micromammals and mesomammals, with a body mass below 5 kg. Mesomammals are included because young individuals may be part of avian and terrestrial predators' diet, and both young and adult individuals may also be a potential prey of humans, as 'small game' (Stiner et al., 2000). Small mammal faunas could be caught ('small game' of slow movement) or trapped ('small game' of fast movements) by humans, most likely near their home ranges (Stiner et al., 2000). Of course, not all small mammal assemblages are attributable to humans, but humans should be considered as a potential source of higher proportions and abundance of these animals when compared to natural/accidental deaths.

Tables of the small mammal abundance at each site are provided in the Supplementary Material. Rodents, didelphids (marsupials) and chlamyphorids (armadillos) are frequent in the studied assemblages. These three groups are susceptible of being hunted by nocturnal and diurnal birds of prey, small carnivore mammals and humans. Chlamyphorids are only considered in the presence/absence analysis, as they are mainly identified by their osteoderms (mostly isolated) instead of dental remains, which can easily drive to the overrepresentation of the armadillos compared to rodents and didelphids. We established the body mass classification showed in Table 4, modified from that used by Terry and Rowe (2015).

Diversity values

Two diversity indexes have been calculated: species richness and dominance. Species richness found in an assemblage depends on its sample size (the number of observed individuals in a population). To solve this problem, rarefaction method was applied (Hammer and Harper, 2006). Rarefaction provides a measure of the species diversity, which is robust to the effects linked to sample size and allows comparisons between communities where animal density is different. In this study, the minimum sample size in which comparisons are possible is 11 individuals for each site. Analyses were carried out using the '*Individual rarefaction analysis*' from the '*Diversity*' menu in PAST (ver. 4.0.3) (Hammer et al., 2001). This software calculates richness values based on the number of different taxa present at each site, without considering their abundance in terms of NISP. Dominance is based on abundance values and the species with the highest abundance are considered dominant in an assemblage. Dominance (D) is calculated through the formula derived from the diversity Simpson index (S): D 1/S (Hammer and Harper, 2006). ¼

Ecoregional analysis through GIS

In order to infer changes in the present dominant ecoregions in the study area, distribution ranges of the species, identified from the International Union for the Conservation of Nature Red List of Threaten Species (IUCN), are intersected with cartography of Terrestrial Ecoregions of the World (TEOW) from WWF (Burkat et al., 1999; Olson et al., 2001) and implemented on software GIS. We follow the principle of the Mutual Ecographic Range (MER) method (Blain et al., 2009, 2016). In other words, ecoregions occupied by the current analogue assemblages of the fossil association recovered from each analysed level are identified and, following methodological uniformitarianism, are extrapolated to past conditions. Species that naturally inhabit the same area (species typically found in the Pampean Region) will overlap their distribution. On the contrary, species that inhabit different areas (e.g. an assemblage with species from the Pampean Region and Patagonia) will not overlap. The overlapping of present distribution areas of the small mammals may be useful to assess more likely environmental conditions occupied by the studied taxa during the past. This analysis allows us to easily detect the presence of assemblages with no present counterpart (Pardinas and Teta, 2000; Quintana, 2001a). Taxa determined at genus level and taxa strongly affected by perturbing parameters (e.g. landscape anthropization), such as *Bibimys torresi*, *Pseudoryzomys simplex*, *Tolypeutes matacus* and *Ctenomys talarum*, were excluded from the analysis, as their current distribution does not represent their true potential ecological/climatic distribution (see Abba and Vizcaíno, 2011; Teta et al., 2014; Pardinas et al., 2017) and would bias the result or fail to provide overlapped areas. The resulting overlapped areas are useful to infer the Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). These values were extracted from the bioclimatic variables 1 and 12, downloaded from the WorldClim database (Fick and Hijmans, 2017).

Habitat Weightings and Chorotype classification

Following the Köppen-Geiger climate classification established by Beck et al. (2018) and the vegetation descriptions included in Cabrera (1976), Soriano et al. (1991) and Oyarzabal et al. (2018), the current habitats proposed for the Pampean Region are described as follows:

a) Steppes/pseudosteppes - temperate grasslands present in the Humid Pampa region. These habitats are mainly constituted by grasses of family Poaceae, such the genera *Nassella*, *Piptochaetium* and *Andropogon*, which may appear accompanied by *Baccharis* and *Eupatorium.* Climate is characterized by low rainfall and temperature variability.

b) Arid/semiarid - vegetation is mainly constituted by xerophilous shrubs, thorn plants and sparse ground vegetation. The main family represented is Zygofilaceae, being *Larrea* the most common genus. The family Cactaceae is also present together with xeric trees of the Fabaceae *Prosopis.* Climate is characterized by low rainfall and greater variations in temperature.

c) Wetlands - permanent rivers, hygrophilous vegetation areas, marshes, swamps, fens and peatlands are included in this category. Some small mammals are highly dependent on the presence of water bodies.

For each small mammal species, its distribution is weighted according to the relative importance of the described habitats (e.g. Evans et al., 1981; Andrews, 2006; Andrews et al., 2016). Based on this method, a species that lives in steppes/pseudosteppes, but also in arid/semiarid environments, without preference for one of them, would be weighted as 0.5 for each habitat. Weighted values for each habitat are multiplied by the abundance of each species represented in the different levels of the archaeological site. Thus, if the abundance of a species shows extreme variations from one level to another, it is possible to evaluate if these variations are related to climate changes or associated to taphonomic processes, such as changes in predator species in the different levels. Scores assigned for the Habitat Weighting method are mainly based on the habitat preferences of the small mammal fauna described by Patton et al. (2015), Gardner (2015) and information included in the IUCN Red List of Threatened Species.

From a biogeographical point of view, it is possible to classify some species into specific groups, sharing common historical or ecological factors (Real et al., 1992). A common distribution pattern of various species can be defined as a 'Chorotype' (Baroni-Urbani et al., 1978). Chorological classification here applied is based on the methodology initially proposed by Marquez et al. (1997), later used to propose a chorological classification for small mammals by Sans-Fuentes and Ventura (2000); this classification has been used in palaeoecological studies to define climatic changes in fossil sites (e.g. Lopez-García et al., 2010; Banuls-Cardona and Lopez-García, 2016). For the characterization of chorotypes in this study, a similarity matrix is constructed, considering the presence or absence of small mammals in the different Köppen-Geiger climates established for Argentina. This is evaluated following the species distribution data provided by the IUCN, Gardner (2015) and Patton et al. (2015). The similarity matrix has been statistically processed using the package 'RMacoqui' (Oliveiro et al., 2015) for R (R Core Team, 2020), which automatically calculates the necessary parameters to establish the different chorotypes (see Sans-Fuentes and Ventura, 2000; Real et al., 2003) and creates a dendrogram in which the different species are classified by their distribution similarities. We established five chorotypes for the modern small mammal assemblages from the Pampean Region, using the nodes of the dendrogram in which p-value < 0.001 (Table 5).

- Chorotype 1 (C1) is related to the cold and mainly arid conditions found at the southern part of the country (BWk). The distribution of this chorotype includes the areas of Espinal, Low Monte and Patagonian Steppe.
- Chorotype 2 (C2) is characterized by the presence of a single taxon, *Reithrodon auritus.* Although it is included by the method in a chorotype 1, we classified this species as a chorotype 2, because it is not only considered an indicator of cold/arid (BWk, BSk) conditions but also a good indicator of temperate/humid ones (Cfa, Cfb). Therefore, it may tolerate a change from humid and temperate conditions to arid and colder ones.
- Chorotype 3 (C3) includes those species present in the Pampa with certain tolerance to semiarid conditions, both hot and cold (BSh, BSk). Their distribution mainly covers the Humid Pampa and part of the semiarid cold Dry Pampa, although it also penetrates the semiarid, hot climate (BSh) in the Chaco Province.
- Chorotype 4 (C4) gathers species from the Humid Pampa climate conditions, which have little or no tolerance to climatic changes (Cfa, Cfb).
- Chorotype 5 (C5) includes species considered generalist, with a wide climatic tolerance, which may present specific requirements in their habitats.

Taxa at genus level are not considered in habitat and chorotype analyses, except for *Ctenomys* sp., found in Laguna Cabeza de Buey 2 and Paso Otero 4. This caviomorph is included due to its exceptional abundance in the sites, contrary to the rest of the species identified at genus level, whose abundance percentages do not provide any relevant information (see tables in the Supplementary Material).

Results and discussion

Diversity and body mass analyses

As previously said, the selected archaeological sites were interpreted as two different taphosystems (Fernandez-Lopez, 1984): open-air sites and rockshelter sites. Open-air sites (Laguna Cabeza de Buey 2, Arroyo Seco 2 and Paso Otero 4) are characterized by low richness (number of recorded species without considering their abundance) and high dominance (diversity of species considering their abundance), while rockshelters (Cueva El Abra and Cueva Tixi) show high richness and low dominance (Fig. 2). A t-student test corroborates these differences between the richness and dominance values for each studied taphosystem, being p- values 0.001. These differences are mainly the consequence of the dominance of fossorial species in open-air sites, such as *Ctenomys* sp. The remains of this taxon would not come only from predation, but part of them could probably come from *in situ* natural death. However, the different preservation context in each taphosystem may have influenced these diversity values. Alternatively, the location of Cueva Tixi and Cueva El Abra in the Tandilia mountain range could also have favoured their higher richness, as this area could have acted as a natural refuge for some of the small mammals recorded in these sites. The higher richness observed in rockshelters is probably related to the favourable physical and chemical environment that caves and rockshelters provide for bone preservation, as well as to their usefulness as protection for predators that bring their prey back to the cave or shelter (Andrews, 1990; Torres et al., 2003). Cave environments maintain a relatively constant temperature and humidity, and accumulated vertebrate remains are considerably protected from weathering and other destructive biotic and abiotic processes, such as trampling, abrasion or compression (Andrews, 1990; Simms, 1994; Behrensmeyer, 1991).

Prey bone assemblages in open-air environments are less spatially restricted and more exposed to different biotic and abiotic processes than they are in rockshelters (Gutierrez et al., 2016). In fact, in open-air sites, robust skeletal remains, such as those from *Ctenomys* sp., have more possibilities of being preserved than the smaller remains, as they are more resistant to processes of trampling, weathering or wind/water dispersal (Montalvo et al., 2020). This fact may favour a better representation of some species against others, affecting the values of diversity (high dominance and low richness). Exceptionally, pellets in open-air environments may be well preserved in dry periods, providing better original diversity values, as it happens when rapid burial occurs since skeletal elements are rapidly protected from meteoric conditions (Andrews, 1990; García-Morato et al., 2019; Montalvo et al., 2020). However, a rapid burial is not explicitly interpreted for the open-air sites here analysed, although natural death of some fossorial species inside their burrows has been suggested for Laguna Cabeza de Buey 2 (Quintana, 2001a, 2016a, 2016b; Alvarez et al., 2013; Gomez, 2014; Scheifler and Messineo, 2016).

Apart from preservation contexts, the agents involved in the production of species record in these sites deserve special consideration. The involvement of specialist predators, which show clear preferences for a particular type of prey, influence diversity values and palaeoecological interpretations. Strigiforms (most frequently the owl *Tyto furcata*, a generalist predator) have been identified as the most likely predator involved in the studied fossil assemblages (Table 3). This strigiform usually hunts within a radius of 1-5 km around its living area (e.g. Lovari et al., 1976;

Taylor, 1994), does not have a favourite prey, although it usually does not take large-sized prey (except when feeding nestlings), and prefers hunting mainly at night in open areas, which favours the detection of its prey (sigmodontine rodents and marsupials). Furthermore, all sites show human involvement and, whenever human presence is intense, a clear dominance of particular species and size categories is observed. These categories are analysed through a Detrended Correspondence Analysis (DCA), to avoid the "arch" effect of the data and compression of the axis scores, which indicates the relative position occupied by each site in relation to the body size distribution (Fig. 3). For instance, small-sized taxa (<170 gr, categories A-C) are abundant in Cueva Tixi and the open-air sites of Laguna Cabeza de Buey 2 and Arroyo Seco 2. In contrast, taxa in Paso Otero 4 and Cueva El Abra are >250 gr (categories D-E). One of the most characteristic traits of the latter two archaeological sites is the high influence of humans. The evidence of butchering and cooking modifications on skeletal elements from Paso Otero 4 (Alvarez et al., 2013) strongly suggests that humans brought these animals purposefully to the site. In Cueva El Abra, some taxa may have been introduced by *Tyto furcata*, but species of higher size categories are dominant, indicating that a different agent is also involved. The caviomorphs *Galea leucoblephara* and *Cavia aperea* (size category D) represent approximately 90% of the assemblage and they were probably introduced by humans (Quintana, 2016a). Human activity would also be the source of these species in levels C and B of Cueva Tixi (*G. leucoblephara* was originally cited as *G. tixiensis* by Quintana, 2001b; Quintana, 2016b), which implies that these levels may have been displaced to the size Category D, but the abundance of cricetid rodents (*Reithrodon auritus*) and didelphids with respect to caviomorph rodents is probably contributing to the worst separation of these two levels. The elevated abundance of cricetid species is probably due to the presence of strigiforms in the site, most likely *Tyto furcata* (Quintana, 2016b) that hunts small-sized mammals such as sigmodontine cricetids and didelphid marsupials.

Ecoregion overlap analysis based on presence/absence data

Results from applying ecoregion overlap analysis indicate that Cueva Tixi presents an assemblage with no modern counterpart (Figs. 4 and 5). In levels lower to D, this is due to the presence of species commonly found in humid environments (i.e. *Holochilus vulpinus*, *Monodelphis dimidiata*), together with other species linked to arid ones, such as the marsupial *Lestodelphys halli*. The latter is restricted today to the Patagonian Region, except for two areas, one in southern Mendoza Province (central-west Argentina) and another in the southern limit of the Pampean Region, both related to the arid conditions of the Low Monte ecoregion (Formoso et al., 2015, and references therein). Despite the absence of overlapping in Cueva Tixi, the species composition from this site indicates that temperate/humid species, such as *Bibimys torresi* and *Pseudoryzomys simplex*, become better represented from levels D to B (Quintana, 2001a).

Although all the studied sites are located in the Humid Pampa, the presence of certain species, such as the armadillo *Zaedyus pichiy,* indicates more arid conditions than today. Abba and Vizcaíno (2011) suggested that *Z. pichiy* penetrated the Humid Pampa during lower precipitation and temperature events. However, this species is present in all the analysed sites and no correlation with possible arid events is found associated to its presence.

Alternatively, as armadillos were frequently consumed by hunter-gatherers in the past, the presence of *Z. pichiy* can be explained as brought by humans and unrelated to climatic conditions. According to ethnoarchaeological observations, humans covered distances of several kilometres, without exceeding 10 km around their camps, to hunt prey below 20 kg (daily food procurement and 'small game') (Binford, 1978; Kelly, 1995; Stiner et al., 2000; Scheifler and Messineo, 2016). Taking this into consideration, *Z. pichiy* could have had a wider distribution than today or was hunted within the border of its present range, being part of an intense hunting selection (amongst micro/mesomammals) that involved other armadillos, such as *Tolypeutes matacus* or *Dasypus hybridus*, and would not indicate therefore the incidence of arid conditions. Only in Laguna Cabeza de Buey 2, the presence of *T. matacus* in levels IV and III is indicative of possible arid conditions, although other faunas linked to a possible arid event have not been detected. No other species typically linked to the Dry Pampa, which do not penetrate the Humid Pampa, have been recorded in the analysed sites. The presence of *Z. pichiy* causes that most of the resulting overlaps are represented by small areas close to, or partially inside the Espinal ecoregion (Fig. 4). Nevertheless, the humid conditions represented by the Pampa ecoregion remain as dominant (Fig. 5) in the analysis, with the exception of Laguna Cabeza de Buey 2 (levels V and II/I) and level AS2-Z of Arroyo Seco 2, in which Patagonian Steppe, Espinal and Low Monte ecoregions are dominant and more arid conditions are inferred (Fig. 5).

Level V of Laguna Cabeza de Buey 2 coincides with the Last Glacial Maximum (LGM) and more arid conditions would be expected. In fact, MAT and MAP of this level indicate colder and arid conditions than the ones observed for the other levels (Fig. 5). Unfortunately, only two species from this level can be used in the overlapping analysis (*Reithrodon auritus* and *Z. pichiy*, because *Ctenomys* sp. is identified at genus level and cannot be included in the analysis, although it is probably hinting more humid conditions). In turn, in the level LCB2-II/I of the same site, the arid conditions (also indicated by a decreased in MAP, Fig. 5) are inferred from the absence of *Holochilus vulpinus*, although another species, *Pseudoryzomys simplex*, is linked to humid chacoan conditions. *Pseudoryzomys simplex* was not included in the overlapping analyses, although it was probably a typical element of the Pampean Region that was regionally extinct due to the intense habitat changes produced by humans (e.g. Teta et al., 2014; Pardinas et al., 2017). Arid conditions inferred for Arroyo Seco 2, level Z, are also probably linked to the LGM (MAP in Arroyo Seco 2 is one of the lowest ones, together with that from LCB2-V, see Fig. 5). Nevertheless, apart from *Z. pichiy*, no other species indicative of arid conditions was found in the levels related to the LGM.

Habitat Weighting and Chorotype classification proposed for Pampean Region

A summary of the results obtained for the Habitat Weighting classification and Chorotype classification is shown in Table 6, which also includes a classification of the species according to their size and their presence/absence in the analysed sites. Figs. 6 and 7 shows the results after applying these classifications to the different faunal assemblages, having in mind their relative abundances.

As it was observed for diversity values (Fig. 2), there are also differences in the representation of chorotypes and habitats depending on the taphosystem (i.e. open-air sites vs. rockshelters). In fact, when data are analysed through a Correspondence Analysis (CA), a clear separation is observed in this sense (Fig. 7). Open-air sites are mostly related to Chorotype 4, while rockshelters are mainly linked to Chorotypes 2 and 3, although in some cases Chorotype 4 yielded similar percentages as Chorotype 3 (Figs. 6A and 7A). In Paso Otero 4 and Cueva El Abra, in which human presence and rodent consumption is identified, Chorotype 5 is well represented when rodents consumed by humans are included (Fig. 7A). Species included in this chorotype show wide ranges of distribution and are mainly associated to large-size categories (Table 6).

Concerning habitat representation, all the sites are mostly characterized by the presence of steppes/pseudosteppes (Figs. 6B and 7B). Rockshelters stand in the analysis slightly separated from open-air sites, as some recorded species in this taphosystem are equally present in steppes/pseudosteppes and arid/semiarid environments (both environments are present today in the analysed area, although the range occupied by each species may have varied through time). The presence of steppes/pseudosteppes and arid/semiarid habitats is also observed for Paso Otero 4. In this site, *Lagostomus maximus* is the best represented species, which is linked to these environments (Fig. 7B, Table 6). However, when *L. maximus* is not considered, steppes/pseudosteppes become dominant (Figs. 6B and 7B). Cueva El Abra also shows a good representation of arid/semiarid environments and wetlands when rodents consumed by humans are excluded from the analysis (Figs. 6B and 7B). In the case of Cueva Tixi, wetlands show an increasing trend, while arid/semiarid environments decrease, probably related to a climatic evolution towards warmer/humid conditions.

The observed differences, especially for chorotypes (Fig. 7A), indicate that both taphosystems are not comparable and their palaeoecology should be analysed separately. The evaluation of changes through levels can easily drive to erroneous interpretations, as the possible changes observed in the chorotypes are not linked to climate but to the preservation conditions. In this study, the species that represent these chorotypes are the same as those included in the highest category sizes and have more robust skeletal elements, susceptible of being easily preserved in open-air sites (Montalvo et al., 2020). Nevertheless, abrupt changes have not been detected for open-air sites or rockshelters. In fact, Cueva Tixi seems to indicate a climatic trend towards present conditions from the Early to the Late Holocene (Fig. 6A). This trend is also observed in the open-air site Laguna Cabeza de Buey 2, but with less resolution and slightly distorted. The other open-air sites reflect more stable conditions through time (Fig. 6A).

Climate changes during the Holocene in the Pampean Region

The absence of abrupt changes in the obtained results contrasts with other authors' results with respect to the general climatic evolution of the Pampean Region. The presence of small mammal species (e.g. *Holochilus vulpinus* and *Scapteromys aquaticus*) associated to subhumid-humid conditions, inferred by pollen analyses (Prieto, 2000; Quattrocchio et al., 2008; Tonello and Prieto, 2010), together with taxa (e.g. *Microcavia australis*, *Lestodelphys halli*) typically linked to more arid/semiarid and cold conditions during the Early Holocene (Pardinas 1999a, 1999b; Tonni et al., 1999; Prevosti and Pardinas, 2001), is only observed in the lower levels of Cueva Tixi. This site contains a typical element of the Patagonian steppes, the marsupial *L. halli*. This species was present in Buenos Aires Province during the Late Pleistocene, associated to cold and dry climatic conditions (Formoso et al., 2015); later, *L. halli* is represented by relict populations from Early to Middle

Holocene, when this species disappeared from the Pampean Region (Formoso et al., 2015). In the level upper of Cueva Tixi, *L. halli* is registered together with *Monodelphis dimidiata*, another marsupial that indicates humid conditions. Nowadays, both species are considered allopatric, as they do not overlap their distributions. Although is tempting to consider the presence of possible climatic pulses linked to the formation of these kind of assemblages, an alternative hypothesis is considered due to the location of Cueva Tixi in the Tandilia mountain range. The two mountain ranges of the Pampean Region, Tandilia and Ventania, are considered 'orographic islands' (Kristensen and Frangi, 1995) that interrupt the typical landscape of the Pampean Region and act as biodiversity reservoirs. A similar situation to that in Cueva Tixi was observed by Goin (2001) in the present Ventania mountain range, who considered this hilly system an ecotone that probably acted as 'refuge' or 'isle' for species such as *L. halli*. The progressive climatic amelioration from colder to warmer conditions observed in Cueva Tixi (Fig. 6A) also supports this hypothesis. However, the incidence of an arid pulse is indicated by pollen analyses (reflecting a dominance of herbaceous psammophytic steppe, with xerophytes and scrub) and other proxies in Paso Otero 4 between 9.8 and 8.9 ka cal BP (Gutierrez et al., 2011). This dry pulse probably affected the surface water quality and water availability; hunter-gatherer groups responded to this event by excavating a water well in Paso Otero 4, to extract subterraneous water, and some small mammal remains have been recovered from the well (Martínez and Gutierrez, 2019). Amongst the small mammal remains are *Lagostomus maximus*, *Ctenomys* sp., *Chaetophractus villosus* and five Caviidae and Cricetidae undetermined specimens. Due to the stratigraphic position of the water well and the presence of *Eutatus seguini* in it, the small mammal assemblage indicated above was interpreted to come from the PO4 Lower level (Alvarez et al., 2013; Martínez and Gutierrez, 2019). All the small mammal species found in the fossil assemblage inhabit steppe/pseudosteppe habitats from the Pampean Region and none indicates the presence of more arid conditions.

Probably, the absence of abrupt changes in the vegetation during the mentioned dry pulse (i.e. the substitution of herbaceous steppes by shrub and xerophytic habitats or the dominance of the latter) is the cause of the absence of abrupt changes in the small mammal fauna composition. Another possible arid climatic pulse during the Early Holocene (between 9000 and 8000 yr BP) was stated by Pardinas (2001), based on the small mammal fauna from Camping Americano site (Buenos Aires Province), in which the presence of *Lestodelphys halli* and *Microcavia australis* would be indicative or more arid conditions.

Pollen analyses for the Middle Holocene indicate subhumid-dry conditions at the southeast of the Pampean Region (Prieto, 2000), while a temperate and humid climate is inferred for the central area during the beginning of the Middle Holocene (Prado and Alberdi, 1999; Pardinas, 1999a, 1999b). However, at the end of the Middle Holocene, the presence of *Microcavia* cf. *M*. *australis* in La Ensenada site (at the northern coast of Buenos Aires Province) could indicate the incidence of arid conditions (Tonni and Cione, 1984). Similarly, the location of Centinela del Mar site, near the coast, might have favoured the entrance of this taxon during a possible dry pulse (Pardinas, 1999a, b). In contrast, the level III of Laguna Cabeza de Buey 2 (4.7 ka) records the oldest presence of the Chacoan sigmodontine rodent *Pseudoryzomys simplex* in the region, a species that indicates the incidence of humid conditions (Scheifler and Messineo, 2016). This species has been suggested to be also probably a typical element of the Pampean Region and therefore its presence in the archaeological sites would not be the consequence of humid pulses (e.g. Scheifler et al., 2012; Teta et al., 2014; Pardinas et al., 2017). This hypothesis suggests a possible lack of niche conservatism (the tendency of species to maintain ancestral ecological requirements) (Wiens and Graham, 2005) that needs to be tested for *P. simplex* and probably for other Pampean species. A preliminary analysis of the niche of *P. simplex* seems to indicate little changes in the species-environment relationship, which allows inferring that this species probably penetrated into the region during the HCO (SGM, unpublished data). On the other hand, palaeoecological inferences through the analysis of sand dunes suggest the presence of several sporadic torrential rainfall periods during Middle to Late Holocene (8.5e3.5 ka BP) in the area (Kruck et al., 2011), which may have also favoured the entrance of *P. simplex*.

In general terms, more humid conditions have been suggested during the Late Holocene in the Pampean Region, inferred from pollen and large and small mammal fauna analyses (Prado and Alberdi, 1999; Gutierrez et al., 2011; Scheifler et al., 2012; Scheifler and Messineo, 2016; Messineo et al., 2019). Nevertheless, some authors indicate that these conditions were not probably the same across the entire Pampean Region and suggest a possible climatic regionalization, with subhumid-humid conditions prevailing in central areas and subhumid-dry conditions in the southwest (Prieto et al., 2004; Quattrocchio et al., 2008; Tonello and Prieto, 2010). The Late Holocene included two climatic events: the MCA and the LIA. The overall climatic trend observed in Cueva Tixi (Fig. 6) towards the present conditions of the Pampean Region covers the period of these events and does not show any climatic perturbation at these times, despite the presence of *Bibimys torresi* in level C, as well as in Cueva El Abra (contemporaneous to the level C), a taxon traditionally linked to the MCA (Pardinas et al., 2010). On the other hand, the LIA was characterized by a change from temperate/humid conditions to cold/arid ones, but species typically linked to more tropical environments (*B. torresi* and *P. simplex*) are still present in level B of Cueva Tixi, with a chronology related to the LIA, whereas taxa adapted to arid/semi-arid environments, mainly indicated by Chorotype 1, are not detected. Nevertheless, taxa such as *Eligmodontia typus* and *Phyllotis* sp. (typical elements of the Dry Pampa and Patagonia) are recorded together with *B. torresi* and *P. simplex* in Centinela del Mar site (0.3 ka cal BP; Pardinas, 1999b; Pardinas and Teta, 2000), possibly favoured by the presence of a connecting corridor of Atlantic coastal dunes (Pardinas, 1999b). None of the mentioned species are present in level B of Cueva Tixi, implying that the effects of the LIA event were not severe in the area and only affected those sites located near the limit of the Dry Pampa or in coastal areas. The mentioned hypothesis of a possible climatic regionalization in the Pampas during the Late Holocene (Tonello and Prieto, 2010) supports this assumption and the role of the Tandilia mountain range as a biodiversity reservoir or ‘orographic island’ (e.g. Kristensen and Frangi, 1995; Zalba and Cozzani, 2004; Echeverría et al., 2017) that would have favoured the presence of these species until their disappearance from the area. Some authors have also suggested the possibility that *P. simplex* and *B. torresi* had a wider distribution during the Late Holocene (e.g. Scheifler et al., 2012; Teta et al., 2014; Pardinas et al., 2017). Nevertheless, the species-environment relationship of these species through time needs to be carefully analysed to test this hypothesis.

Conclusions

1. The results presented in this paper provide new palaeoecological and palaeoclimatic data for the

Pampean Region (Argentina), using a methodology applied in European sites and adapted for the first time to this South American area. The application of these analyses to other Argentinean regions may provide new information to contrast the obtained results.

2. The analysis of the small mammal faunas from the five selected Holocene archaeological sites shows that the assemblages from rockshelters (Cueva Tixi and Cueva El Abra) present higher values of diversity and abundance (dominance/richness) than those from open-air sites (Laguna Cabeza de Buey 2, Arroyo Seco 2 and Paso Otero 4). This could be the consequence of the spatial restriction in caves, as they favour superimposed and continuous occupation by different predators in a limited emplacement. Open-air sites have not such a spatial restriction and fossil assemblages are more disperse and scant. Post-depositional destruction and dispersal of skeletal elements are greater in open-air sites than in caves.

3. Human activity is confirmed as an important taphonomic agent

that could cause distortive effects in palaeoecological interpretations, increasing the number of small mammal prey with larger sizes (caviomorphs rodents and armadillos). Humans acted as selective predators, searching/trapping for specific mesomammals in the vicinity of the site, although they did not have any preferred hunting area. However, barn owls probably alternated in the site with humans as a low grade of digestive corrosion has been found in some skeletal elements. Sedimentation rates (time-averaging or palimpsets) do not distinguish when only one predator or both simultaneously occupied the site.

4. The sites Cueva El Abra and Paso Otero 4 show intense human activity that influenced the composition of the small mammal faunas. Other sites with evidence of human influence (presence of induced damage on large mammal bones and stone artefacts), such as Arroyo Seco 2 and Laguna Cabeza de Buey 2, do not show a clear influence on the small mammal representation, although the human burials in Arroyo Seco 2 may have altered the levels of the site, affecting the diversity and the dispersion of the small mammal remains. Finally, despite the upper units of Cueva Tixi show certain influence of human activity, the species and dominance/richness of this karstic taphosystem are apparently not modified (at least not significantly) by human activities.

5. Chorotypes and habitat interpretations also show clear differences for open-air and rockshelter taphosystems. While open- air sites are mainly dominated by Chorotype 4 and steppes/ pseudosteppes, rockshelters show a predominance of Chorotype 2 and seem to indicate a possible climate trend towards present conditions (from colder to warmer). This is also observed in the open-air site Laguna Cabeza de Buey 2, but with lower resolution and slightly distorted. The best record of Chorotype 4 in open-air is probably due to the dominance of species with more robust skeletal elements, linked to fossorial taxa.

6. The archaeological sites analysed in this work do not show important variations in their small mammal composition, despite abrupt climate changes are considered responsible for faunal changes detected in other coastal Argentinean sites (especially during the MCA and LIA). Results indicate a consistent trend towards a warmer climate and subhumid-humid/ subhumid-dry conditions, better observed in Cueva Tixi whereas the remaining sites indicate climatic stability. The prevalence of grassland ecosystems during the Holocene in the Pampean Region may have favoured the absence of important changes in the composition of small mammal communities through time. However, taphonomic processes may have played an important role in open-air sites, obliterating possible

climatic events, and decreasing the small mammal fauna diversity. On the other hand, it cannot be discarded that the effects of these climatic variations in the study area were not as severe as it could be expected, due to a possible climatic regionalization, previously indicated from pollen analyses.

Author statement

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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

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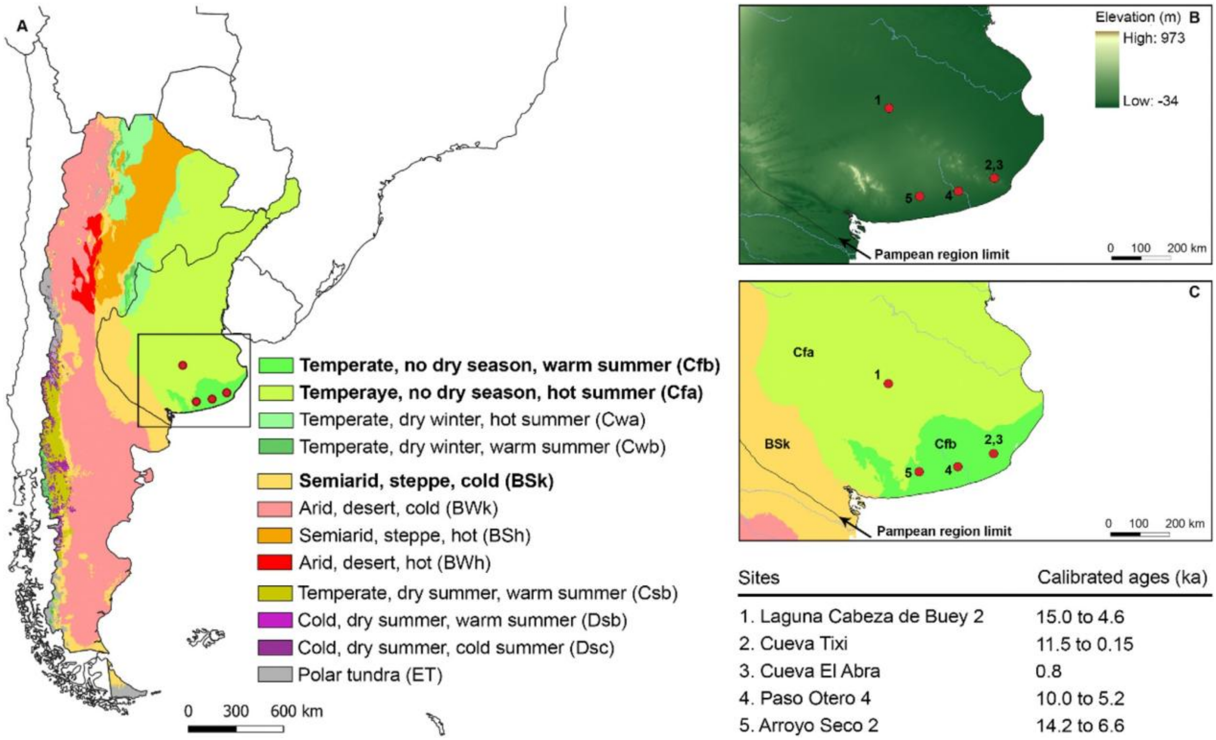

Sites	Calibrated ages (ka)
1. Laguna Cabeza de Buey 2	15.0 to 4.6
2. Cueva Tixi	11.5 to 0.15
3. Cueva El Abra	0.8
4. Paso Otero 4	10.0 to 5.2
5. Arroyo Seco 2	14.2 to 6.6

Fig. 1. A) Map depicting the Köppen-Geiger climate classification for Argentina (Beck et al., 2018). Situation of the studied Pampean archaeological sites depicted in both B) topographic map and C) climate classification map. The limit between Dry and Humid Pampas is indicated by the colour change from yellow (Dry) to green (Humid). The black line in B and C delineates the Pampean Region.

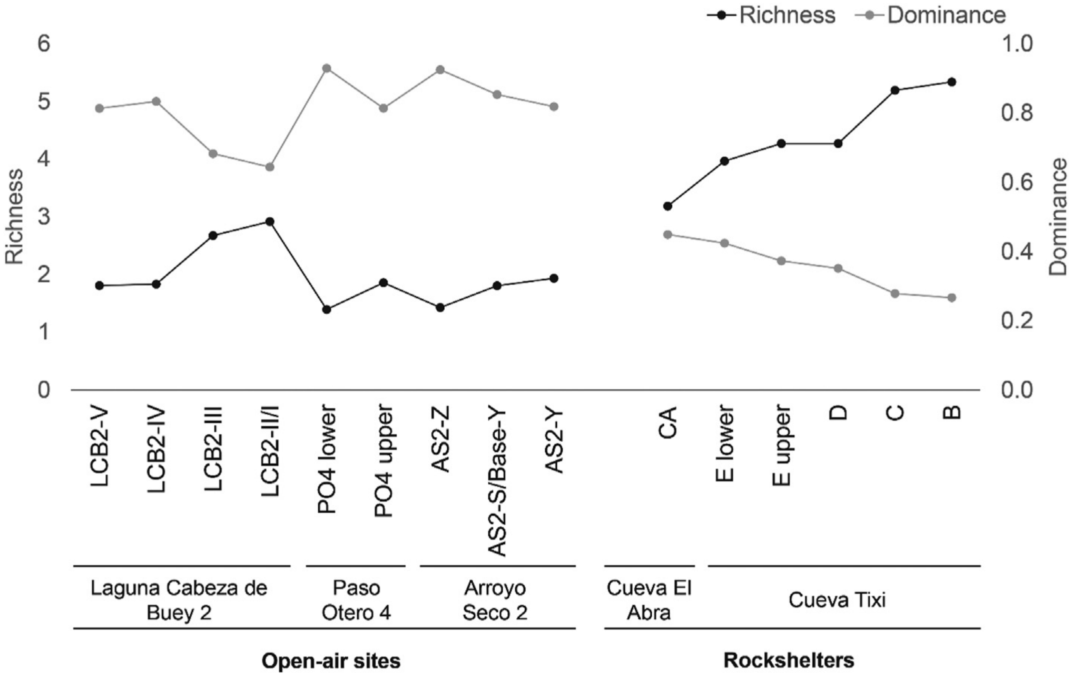

Fig. 2. Species richness and dominance calculated for each level of the analysed sites (Table 1). A minimum sample size of 11 individuals was used according to rarefaction results.

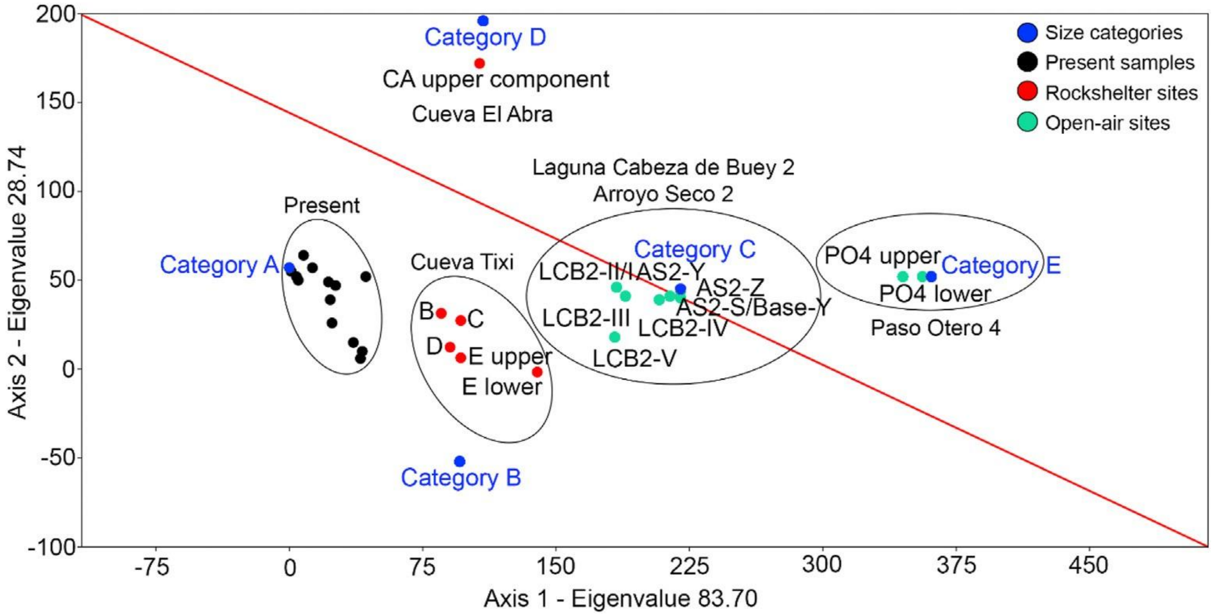

Fig. 3. Detrended Correspondence Analysis for the number of count rodent specimens of each size category from each site (A (0-40 gr), B (40-80 gr), C (100-170 gr), D (250-500 gr), E (>500 gr)); see body mass classification in Table 4. Red line separates the sites with the highest sizes. Component 1 (Axis X) explains 83.70% of the variance. Component 2 (Axis Y) explains 28.74% of the variance. Data of modern samples from the Pampean Region came from Tiranti (1992), Fernandez et al. (2012), Solaro et al. (2012) and Quintana (2015). Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

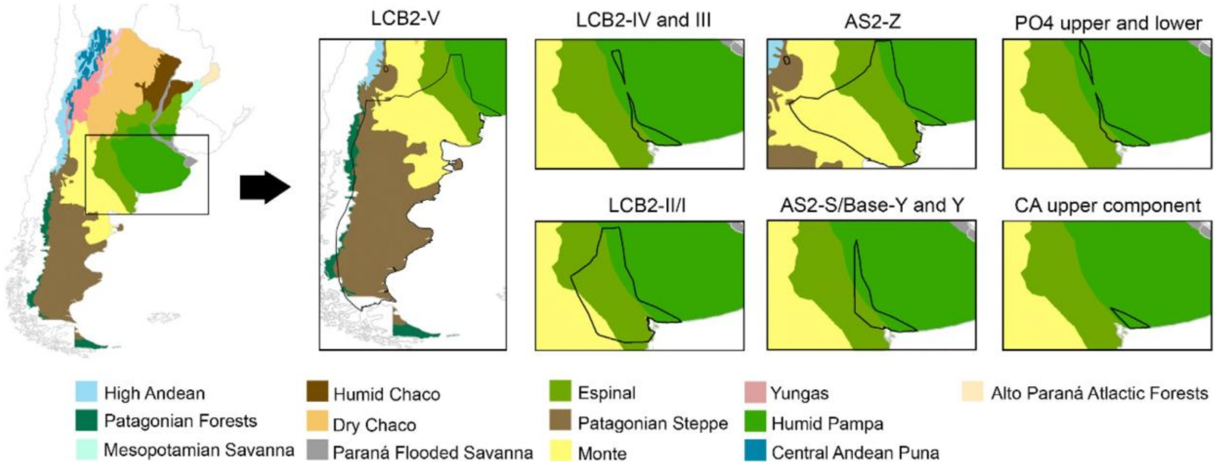

Fig. 4. Overlapping small mammal assemblages in the ecoregion analyses. Maps show the levels of the sites in which overlapping is produced and the area (black line) delimited by the overlapping. The overlapping is produced near the Espinal and Low Monte ecoregions due to the presence of *Zaedyus pichiy*, whose distribution is restricted today to the southernmost part of the Pampa ecoregion. Note that the map of Cabeza de Buey (LCV2-V) shows almost all Argentina due to the high incidence of Patagonian steppe that extends to Tierra del Fuego. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

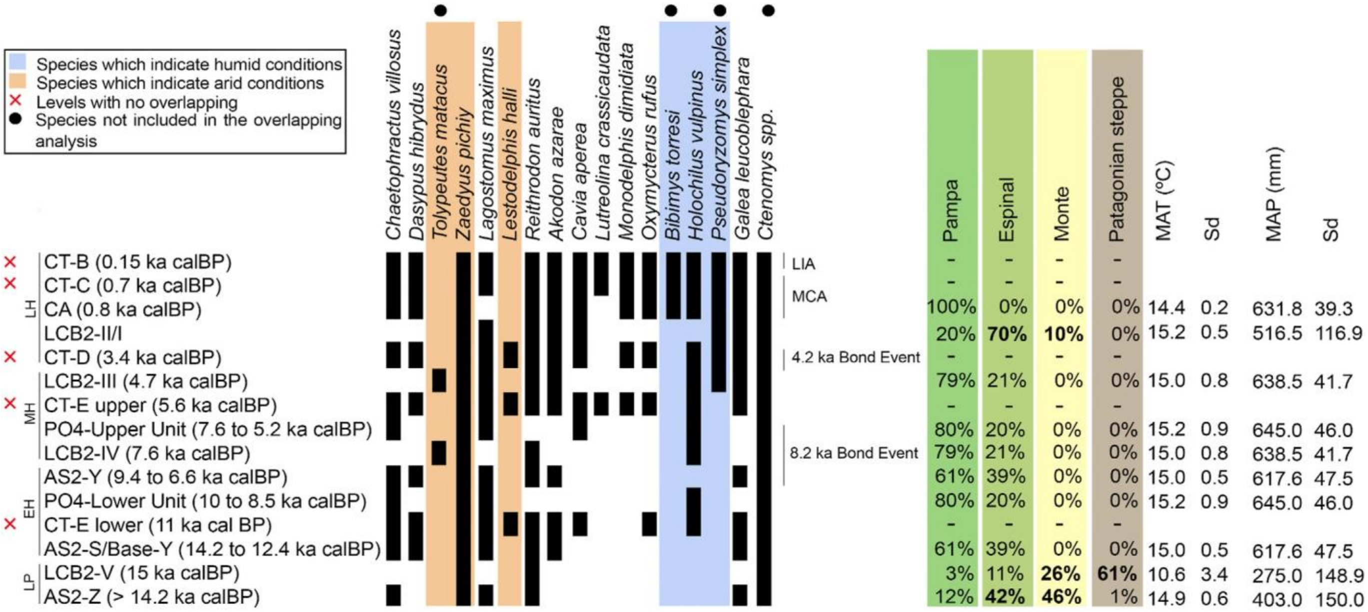

Fig. 5. Presence/absence data ordered through time to check correlation of faunal changes with climatic events and percentage of the different ecoregions included in the overlapping areas. These percentages are calculated using ArcMap 10.5. Bold percentages indicate the dominance of arid/semiarid ecoregions. Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) have been calculated for each overlapping area. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2. NH, Northern Hemisphere.

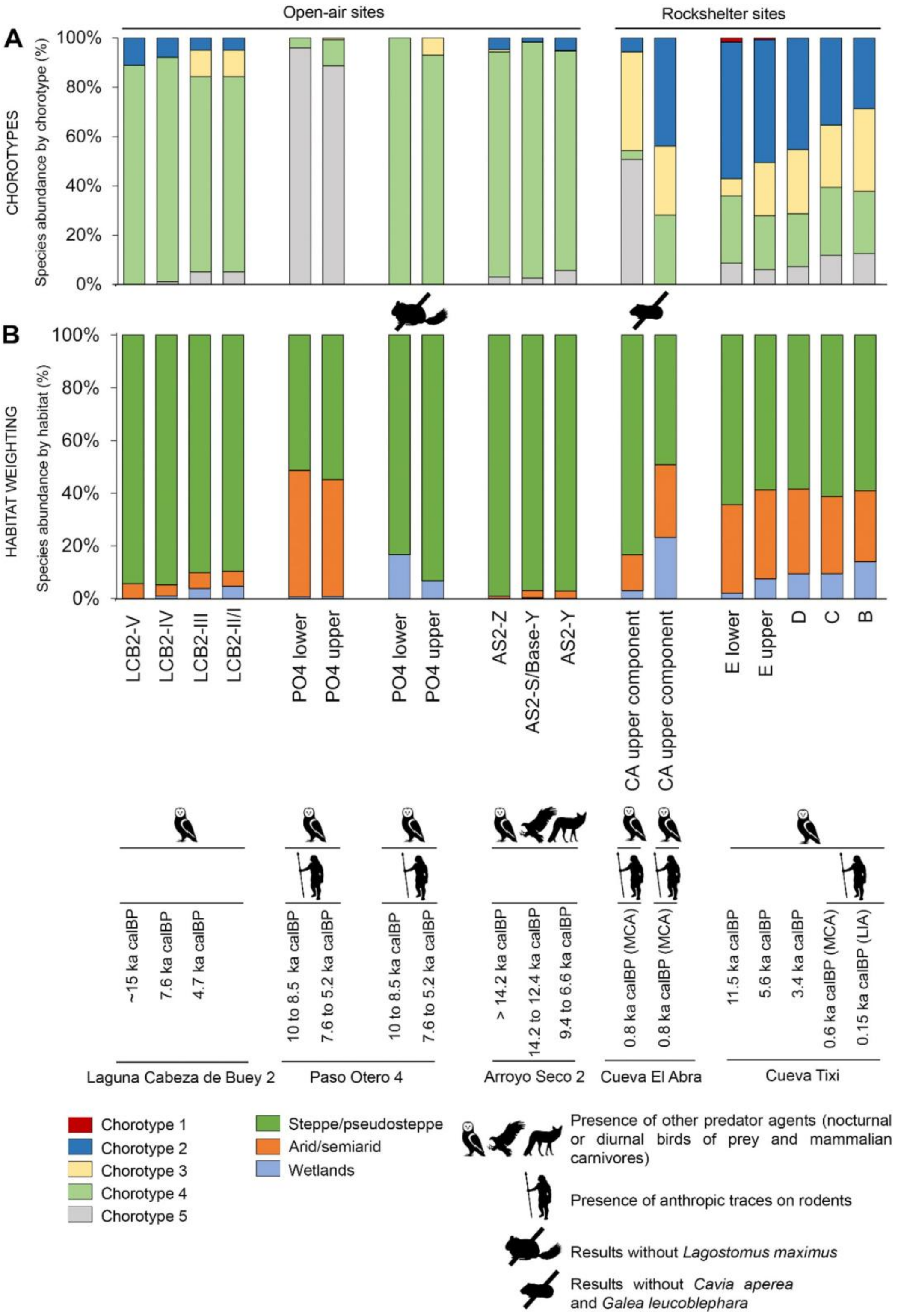

Fig. 6. A) Chorological and B) habitat weighting classification evaluating the changes in small mammal abundance throughout the levels at each site. Human consumption of rodents and the action of other predation agents have been highlighted in the corresponding levels. Two sequences are added for Paso Otero 4 and Cueva El Abra, one considering the rodents consumed by humans and the other excluding them.

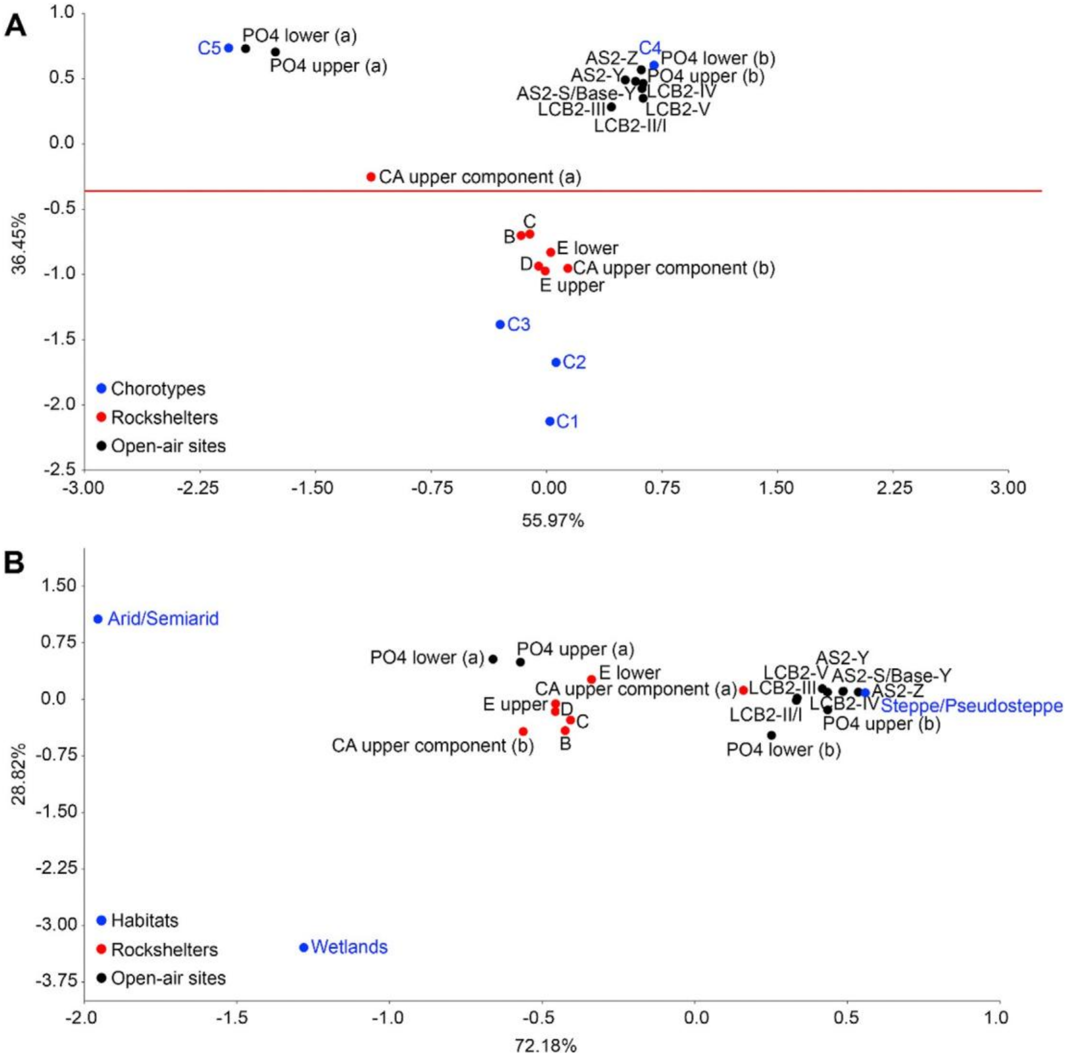

Fig. 7. A. Correspondence Analysis for chorotype classification. Red line separates sites with a dominant chorotype. B. Correspondence Analysis for habitat weighting. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2. For CA and PO4, (a) and (b) refer to included and excluded consumed rodents, respectively (i.e. *Lagostomus maximus*, *Galea leucoblephara* and *Cavia aperea*) (Alvarez et al., 2013; Quintana, 2016a).

Table 1. Summary of the taxa identified for each level of the analysed sites, together with their Number of Identified Specimens (NISP). Data include rodents, didelphids (marsupials) and chlamyphorids (armadillos). See Supplementary Material for detailed information. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

Site	Level	Taxa identified at species level	Taxa identified at genus level	Total NISP	References
LCB2	LCB2 II/I	7	2	184	Scheifler and Messineo (2016)
	LCB2 III	8	2	271	
	LCB2 IV	4	2	124	
	LCB2 V	2	1	30	
CA	Upper Component	13	3	958	Quintana et al. (2003), Quintana (2016a)
CT	B	15	3	1022	Quintana (2016b)
	C	15	4	1698	
	D	14	5	1596	
	E upper	14	4	4096	
	E lower	12	5	837	
PO4	PO4 upper	5	1	1069	Alvarez et al. (2013)
	PO4 lower	4	1	834	
AS2	AS2-Y	8	0	2214	Gomez (2014)
	AS2-S/Base-Y	8	0	979	
	AS2-Z	6	0	978	

Table 2. Studied archaeological sites, showing their levels and calibrated ages (Age ranges and Median probability 2s). Radiocarbon ages from PO4 and AS2 were obtained with different methodologies according to the references. Dates have been calibrated through CALIB 8.20 program (Southern Hemisphere calibration curve [SHCal20], Hogg et al., 2020). Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

Site	Level	^{14}C yr BP	Age range 2s (ka)	Median probability 2s (ka)	Correlated global climatic fluctuations (correlation, this paper)	References
LCB2	LCB2 II/I	-	-	-	-	Scheifler and Messineo (2016); Messineo et al. (2019)
	LCB2 III	4150 ± 42	4519-4824	4.6	-	
	LCB2 IV	6801 ± 40	7568-7681	7.6	8.2 ka Bond event	
	LCB2 V	12,612 ± 1020	12,619-17,934	15.0	-	
CA	Upper Component	958 ± 52	732-925	0.8	MCA - Precolumbian	Quintana et al. (2003), Quintana (2016a)
CT	B	170 ± 80	0-301	0.15	LIA - European conquerors	Quintana (2016b)
	C	715 ± 45	555-676	0.6	MCA - Precolumbian	
	D	3255 ± 75	3314-3594	3.4	4.2 ka Bond event	
	E upper	4885 ± 85	5440-5751	5.6	-	
	E lower	10,045 ± 95	11,240-11,784	11.5	-	
PO4	PO4 upper	4561 ± 41	5038-5318	5.2	8.2 ka Bond event	Alvarez et al. (2013)
		5559 ± 43	6269-6404	6.3		
		6739 ± 48	7476-7668	7.6		
	PO4 lower	7729 ± 48	8391-8554	8.5	-	
		8913 ± 49	9756-10,187	10.0		
AS2	AS2-Y	8461 ± 74	9267-9542	9.4	8.2 ka Bond event	Politis et al. (2016); Politis et al. (2019); Politis (pers. com)
		8390 ± 410	8349-10,297	9.3		
		7836 ± 69	8411-8779	8.6		
		7747 ± 56	8396-8595	8.5		
		7540 ± 80	8165-8453	8.3		
		7388 ± 74	8015-8342	8.2		
		5793 ± 64	6400-6679	6.6		
	AS2-S/Base-Y	12,240 ± 110	13,798-14,556	14.2	-	
		10,500 ± 90	11,999-12,635	12.4		
	AS2-Z	>12,500			-	

Table 3. Characteristics of the main predators identified for the studied sites. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

Site	Level	Possible accumulation agent	Habits and diet	Reference
LCB2	LCB2 II/I LCB2 III LCB2 IV LCB2 V	Strigiforms (low level of digestion observed).	Strigiforms are usually nocturnal birds of prey. Mainly consume sigmodontine rodents. *Athene cunicularia* and *Asio flammeus*, also show diurnal habits.	Scheifler and Messineo (2016)
CA	Upper Component	Human predation only on caviomorphs and *Tyto furcata* on the rest of the small mammal assemblage.	*Tyto furcata* presents nocturnal/ crepuscular habits. Mainly consumes sigmodontine rodents. Humans are specialist predators.	Quintana et al. (2003); Quintana (2016b)
CT	B C	Human predation only on caviomorphs and *Tyto furcata* on the rest of the small mammal assemblage.	*Tyto furcata* presents nocturnal/ crepuscular habits. Mainly consumes sigmodontine rodents. *Athene cunicularia* also shows diurnal habits. Humans are specialist predators.	Quintana (2016a)
	D E upper E lower	*Tyto furcata*.	*Tyto furcata* presents nocturnal/ crepuscular habits. Mainly consumes sigmodontine rodents. *Athene cunicularia* also shows diurnal habits.	
PO4	PO4 upper PO4 lower	*Tyto furcata* and human predation.	*Tyto furcata* presents nocturnal/ crepuscular habits. Mainly consumes sigmodontine rodents. Humans are specialist predators.	Alvarez et al. (2013)
AS2	AS2-Y AS2-S/Base-Y AS2-Z	Nocturnal and diurnal birds of prey and small mammalian carnivores. Possible human intervention.	Generalist predators together with humans which are considered specialist predators.	Gomez (2014)

Table 4. Body mass distribution of the specimens (NISP) from each level of the analysed sites. Abbreviations: LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

Sites	Levels	Category A	Category B	Category C	Category D	Category E
		0 - 40 gr	40 - 80 gr	100 - 170 gr	250 - 500 gr	>500 gr
LCB2	LCB2-II/I	15	12	122	8	1
	LCB2-III	16	19	169	5	1
	LCB2-IV	0	8	92	1	0
	LCB2-V	0	9	24	0	0
CA	CA upper component	15	28	14	386	0
CT	CT-B	294	376	58	126	30
	CT-C	354	685	153	208	55
	CT-D	374	760	166	125	4
	CT-E upper	777	2155	476	300	10
	CT-E lower	41	487	193	58	31
PO4	PO4 upper	0	0	14	1	118
	PO4 lower	0	0	6	0	144
AS2	AS2-Y	4	90	1577	2	96
	AS2-S/Base-Y	7	39	747	5	19
	AS-Z	0	16	927	3	22

Table 5. Chorotypes and climate data established for modern small mammal assemblages from the Pampean Region. See Fig. 1 for the Ko€ppen-Geiger climate classification and ab- breviations. MAT, Mean Annual Temperature; MAP, Mean Annual Precipitation.

Chorotype	Köppen-Geiger climate	MAT (_C)	MAP (mm)
C1	BWk (Arid, cold)	<14	<400
C2	BWk, BSk, Cfa, Cfb (Arid, cold to Temperate, warm)	≤16	≤900
C3	Cfa, Cfb, BSh, BSk (Temperate, warm to semiarid hot/cold)	≥14	≥900
C4	Cfa, Cfb (Temperate, warm)	~18	~1000
C5	Generalist	-	-

Table 6. Small mammal fauna from the archaeological sites classified by chorotypes and habitat. Abbreviations: A/SA, arid/semiarid; St/PSt, steppes/pseudosteppes; W, wetlands; LCB2, Laguna Cabeza de Buey 2; CA, Cueva El Abra; CT, Cueva Tixi; PO4, Paso Otero 4; AS2, Arroyo Seco 2.

			Habitat weighting			Presence				
Species	Chorotype	Size category	St/PSt	A/SA	W	LCB2	CA	CT	PO4	AS2
Lestodelphys halli	C1	B	0	1	0			X		
Zaedyus pichiy	C1	D	0	1	0	X	X	X	X	X
Reithrodon auritus	C2	B	0.5	0.5	0	X	X	X		X
Lutreolina crassicaudata	C3	D	1	0	0			X		
Monodelphis dimidiata	C3	B	0.4	0	0.6		X	X		
Akodon azarae	C3	A	0.5	0.2	0.3	X	X	X		X
Cavia aperea	C3	D	1	0	0		X	X	X	
Oxymycterus rufus	C3	B	0.6	0.4	0	X	X			
Tolypeutes matacus	C3	D	0.2	0.8	0	X				
Bibimys torresi	C4	A	0.3	0	0.7		X	X		
Ctenomys talarum[a]	C4	C	1	0	0	X	X	X	X	X
Holochilus vulpinus	C4	C	0	0	1	X	X	X	X	
Pseudoryzomys simplex	C4	B	1	0	0	X	X	X		
Dasypus hybridus	C4	D	1	0	0			X		X
Galea leucoblephara	C5	D	0.8	0.2	0	X	X	X		X
Lagostomus maximus	C5	E	0.5	0.5	0	X		X	X	X
Chaetophractus villosus	C5	D	0.5	0.5	0	X	X	X	X	X

[a] Instead of *Ctenomys talarum*, *Ctenomys* sp. is recorded at Laguna Cabeza de Buey 2 and Paso Otero 4; several species of this genus are currently found in the Humid Pampa; in this work, *Ctenomys* is placed in Chorotype 4 with preference for steppe/pseudosteppe habitats.