



Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

What happened when the Pleistocene megafauna became extinct?

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ARTICLE INFO

Article history:

Received 26 October 2016

Received in revised form

27 December 2017

Accepted 6 January 2018

Keywords:

End Pleistocene
Massive extinctions
Pampa-Patagonia
Human agency

ABSTRACT

This work presents an updated revision of the information about Pleistocene fauna records in archaeological sites of the Pampa and Patagonian regions of South America. The purpose is to assess the role played by humans within the extinction process of Pleistocene mammals in the South Cone and the effects that the disappearance of Pleistocene large mammals had in human populations which colonized both regions. This is based on the theory of “Broken Zig-Zag”, which considers that the process was gradual in time and in different species, taking place between 15 Ka BP and 8.5 Ka BP in Patagonia and during a longer period, until ca. 7.5 Ka BP in Pampa. For this aim it was considered all those sites with accurate chronological and taxonomic information about the presence of extinct species of mega and large mammals of xenarthrans, camelids, equids and carnivores. Thus, the work is focused on three analytical lines: regional analysis of radiocarbon records of first and last taxonomic appearance, ecology and etiology of species with archeological record and variability of associations of the archaeofauna with material culture. We discuss how the first humans took possession of Pampa and Patagonian regions during and after the last part of the continental extinction process. Thus, there is a contribution with new hypotheses about the differential use of the extinct fauna in both regions. This interdisciplinary approach of social and environmental agency has not been considered in the specialized bibliography so far; therefore novel information is given for interpreting the way in which humans took possession of the fauna, not only as subsistence resources but also as other important agents in the socio-economic and symbolic relationship of humans with the landscape. On the whole, the final result is that the gregarious species of large herbivores (camelids) were the most important resources for hunter-gatherers from the beginning of human colonization. The extinct fauna influenced subsistence complementarily, though it played an important role in the social and symbolic spheres.

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1. Introduction

The extinction of Pleistocene megafauna and other large and small mammals in America is a topic that has already been discussed academically for more than a century regarding the factor(s) which produced such process. The main ideas were being outlined dissimilarly about the role the first humans played in such extinctions when they entered the new world. In the last years, the most widely accepted hypothesis is that the finipleistocenic extinctions are considered as a process of deep changes, temporarily long and environmentally heterogeneous, where the human impact about the faunas was collateral.

On the other hand, every new archaeological finding referred to

that period of time introduces new questions about the level of human-fauna interaction in such a complex process that began operating at the end of the Pleistocene and that in some regions like Pampa, lasted until mid Holocene (Martínez and Gutiérrez, 2011; Martínez et al., 2016). The main role given to humans in the extinction process was due to findings of large sites of mammoth and bison slaughter that, since the first decades of the 20th century, have been carried out in North America. Thus, the scenario and role of the first settlers in the continent may have been magnified as regards the excessive hunting of mega and large mammals, with the minimization of the small species hunting and collection of animal and vegetable products (Sellards et al., 1947; Wormington, 1957). In this sense, and together with the progression of a programme of systematic archaeological excavations in sites of first Americans from the great North America plateaus, in the 1970s the main ideas about human-megafauna interactions were stemmed in three hypothesis lines: 1) That of an intensive human exploitation

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of the Pleistocene fauna which provoked the fast extinction by “Overkill or blitzkrieg” (Martin, 1973, 2005), here the humans could have been the main cause of extinctions; 2) a scenario of scarce interaction of humans hunting those mega faunas, and where it is understood that the deep postglacial environmental changes were mainly responsible for the fauna extinctions (Bryan, 1978; Guthrie, 1984). Finally, 3) where the humans may have been another factor in the extinction process but not the main one. Their role could have been that of a catalyst or “coup de grace” that boosted the extinction of animal populations that, due to environmental changes at the end of Pleistocene, were already in clear numerical regression (Guilday, 1984; Miotti and Salemme, 1999; Cione et al., 2009; Metcalf et al., 2016).

More thorough studies and in more extended regions in South America allow highlighting another observation, presented by Alan Bryan (1986, 1995) but dodged by many, which lies on the principle of the huge environmental and cultural variability of the end of the Pleistocene in North and South America. This key idea made us redirect our exploration to the southern portion of the continent and thus formulate new ideas about the ways in which the first humans explored, got in contact with the great variety of environments in South America and finally, colonized the continent (Miotti, 2003; Miotti and Marchionni, 2012). Now, in the light of new paleo-environmental and archeological information, the most moderated hypothesis to explain the scenario of mega-mammal and large mammal extinction in South America, close to the Pleistocene–Holocene transition, seems to be that summarized in the “Broken Zig-Zag” theory (Cione et al., 2003, 2009, 2015; Prado et al., 2015; Metcalf et al., 2016; Politis et al., 2016).

This is based on the special fauna structure of South America, stemmed partly from the impact produced by the Great American Biotic Interchange (GABI); its confirmation was obtained from Pampa archeological sites towards Pleistocene and beginning of Holocene, which present a prevalence of xenarthrans in the megafauna; the scarce representation of the total diversity of the extinct mega-mammals and large mammals in the archeological sites, and in short the extinct mega-mammals and large mammals are part of GABI in South America. In this background Cione (Cione et al., 2009) consider that humans participated in the GABI, but they were not the main actors. In this sense, this hypothesis is in concordance with our works in Pampa and Patagonia (Miotti, 1998; Miotti and Salemme, 1999, 2004; Miotti and Marchionni, 2012; Salemme, 2014).

In those works, we proposed that the first settlers of Pampa and Patagonia could have had a generalized or broad spectrum hunting-gathering strategy, and that at the end of the early Holocene and at the beginning of Holocene they could have started to change it towards a specialized one, mainly based on the exploitation of the species *Lama guanicoe* (guanaco) (Miotti and Salemme, 1999). In the light of the information that is presented herein, it is perceived that such change could have happened previously, when Pampa and Patagonia peopling was still in early development. Therefore, in this work we carry out an updated and re-assessed summary of the available information about the record of Pleistocene species, whose survival until early Holocene allows suggesting a longer use of some species in both regions aforementioned. In this case, even though the environmental changes must have been of great impact in each region for the disappearance of mega-mammals, the purpose of this work is to approach new ideas about the kind of appropriation performed by human groups and as a consequence, to bring up for discussion the human impact about extinctions. To achieve these objectives, the contextual archaeofauna and archeological information has been brought into play. This information allows better understanding of the social and symbolic impact, beyond that ecological and economic of the humans who

colonized Pampa and Patagonia. In that sense, this new information contributes to re-assess the hypothesis about the megafauna extinction and its environmental and social consequences in Pampa and Patagonia, to support the variability of forms that this process had in different latitudes, and finally, to evaluate human-megafauna interactions and the impact that its disappearance had in different regions for the first settlers, not only in terms of economic resources but also social and symbolic resources.

2. Background and methodology

The reference framework used here is that of zooarcheology, taphonomy and biogeography of updating basis and regional scale. These parameters are the most suitable for the data analysis necessary for drafting the relationship trends between the first humans and faunas, as well as the concept of changes of human appropriation in different paleo-environmental scenarios. Both in Pampa and Patagonia the advances produced in the paleo-environmental reconstruction, either from the study of archaeofaunas or from several environmental proxy, and from the use that humans made of the fauna resources, have been outstanding in the last decades. However, in order to delve into the ways hunter-gatherers developed for appropriating new resources, it has also been considered the ethology and ecology of species with archeological record and corresponding to Lujanian fauna (40 Ka¹ BP to 7.5 Ka BP).

The study of the recorded species behavior is an important tool for relating the trends of the use of different weapons and hunting strategies (collective or solitary; by encounter or by lurking). In that sense, the assumption is that the most recurrent species in the archeological sites were those that fitted most the hunting techniques. For defining the use or human coexistence with different species throughout the transition Pleistocene–Holocene and early Holocene, the dates of the first and last appearance of the main Pleistocene mammals with archeological record were considered.

The selected sites are grouped in four time blocks (Fig. 1 and Tables 1 a, b and 2) that involve the contexts of hunter-gatherer societies populating both regions during the “Colonization” phase (13–8.5 Ka BP), which includes “scouting” and choice of new environments for inhabiting (Meltzer, 2003; Rockman, 2003; Miotti, 2008; Miotti et al., 2015), and the “Territorial consolidation” phase (8.5–4.5 Ka BP) *sensu* Miotti (2003) and Miotti and Salemme (1999, 2004); or colonization phase *sensu* Borrero (1990).

Calculations of taxonomic diversity/abundance with the purpose to evaluate the use of fauna in both regions was carried out based on a Ntaxa of each site. This is due to the fact that NISP values are only available for some of the researched contexts, and therefore, even though the production of more specific abundance indexes such as diversity (d1), and richness (H') indexes (Grayson, 1984) would provide a better definition to tendencies, data quantification in this parameter becomes very heterogeneous in different sites of both regions. Finally, to evaluate the social and symbolic impact that the disappearance of large mammals and mega-mammals could have had among the first settlers, contextual archeological markers were taken beyond the zooarcheological data. These are rock art as well as specimens of special anatomic portions of certain animals, such as paws and teeth of large carnivores, scutes of glyptodonts and leather of mylodonts (Taçon et al., 1996; Politis and Saunders, 2002; Miotti and Carden, 2007).

For this work it has been chosen 45 zooarcheological contexts of Pampa and Patagonian (Chilean and Argentinian) regions, whose human settlements correspond to the transition Pleistocene–

¹ Ka BP is considered in ¹⁴C years before present.

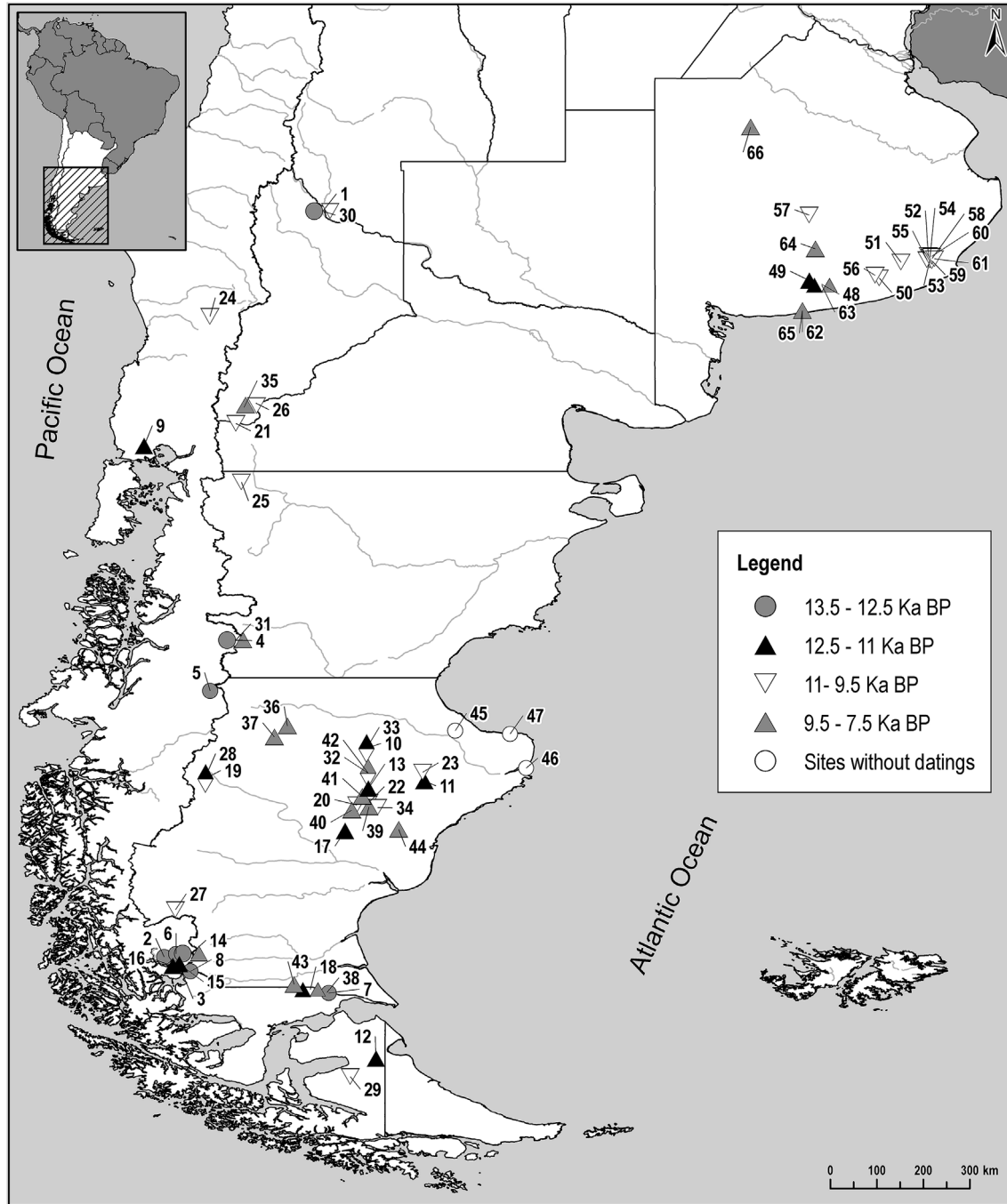


Fig. 1. Geographical distribution of the archaeological and paleontological sites: 1, 30. Huenul; 2, 15. Milodón cave; 3. Lago Sofia-4; 4, 31. Baño Nuevo-1; 5. Las Guanacas; 6, 14. Lago Sofia-1; 7. Los Chingues; 8, 16. Cueva del Medio; 9. Monte Verde; 10, 33. Los Toldos-Cave 3; 11, 23. Piedra Museo-AEP-1; 12. Tres Arroyos; 13. Cerro Tres Tetras; 17. Casa del Minero-1; 18, 38. Fell; 19, 28. Cerro Casa de Piedra-7; 20. La Gruta-1; 21. El Trebol; 22. Túnel; 24. Mariflo; 25. Epullán Grande; 26. Cuyín Manzano; 27. Chorrillo Malo-2; 29. Marazzi; 32, 42. Maripe; 34. El Ceibo-7; 35. Trafal-1; 36. Arroyo Feo; 37. Cueva de las Manos; 39. La Mesada; 40. La Martita; 41. El Verano; 43. Las Buitreras; 44. Cerro Bombero; 45. Fitz Roy; 46. Puerto Deseado; 47. Bahía Sanguineto; 48, 49, 63. Arroyo Seco-2; 50. Paso Otero-5; 51. Cerro La China; 52. Tixi; 53. Los Pinos; 54. Amalia; 55. Burucuyá; 56. Paso Otero-4; 57. Campo Laborde; 58. Lobería-1; 59. Los Helechos; 60. El Abra; 61. La Brava; 62, 65. El Guanaco; 64. La Moderna; 66. Laguna de los Pampas.

Holocene, early Holocene and mid Holocene (Fig. 1 and Tables 1 and 2), and where remains of Pleistocene fauna have been found.

3. The great biotic interchange. Implications of the holartic species in Pleistocene extinctions in South America

Around three million years ago, when the terrestrial bridge between North America and South America was linked (Cione et al.,

2015), the last stage of the great biotic interchange between North American and South American subcontinents took place (GABI). During this interchange, numerous mammal families of the Holarctic Region emigrated to South America. The immigrant mega mammals (heavier than 1 ton) were only the Gomphoterids, while the large mammals (heavier than 44 kg) included ursids, tayasuids, equids, camelids and cervids, among other felids (Cione et al., 2009). Regarding the native fauna from South America, xenarthrans

Table 1
Frequencies of extinct and living mammals at archaeological sites in Patagonia region.

#	PATAGONIA sites showed in Fig. 1	¹⁴ C dating	Frequencies of species			References
			living	extinct	total Nsp	
1	Huenul cave	13,840 ± 56–11,841 ± 56	1	1	2	Barberena et al., 2015, Pompei et al., 2012
2	Milodón cave	13,630 ± 50–12,000±	1	5	6	Martin, 2013
3	Lago Sofia 4 cave	13,400 ± 90–11,590 ± 100	8	5	13	Martin, 2013
4	Baño Nuevo 1 cave	13,480 ± 35–11,240 ± 40	1	2	3	Mena and Reyes, 2001
5	Las Guanacas rockshelter	13,275 ± 50	3	5	8	Labarca et al., 2008;
6	Lago Sofia 1 cave	12,990 + 490	1	2	3	Borrero et al., 1997
7	Los Chingues cave	12,165 + 80	1	3	4	Martin, 2013
8	Cueva del Medio	12,720 ± 300	1	1	2	Nami and Nakamura, 1995
9	Monte Verde	12,500± –11,800±	2	3	5	Dillehay, 1997
10	Los Toldos cave 3 layer 11	12,600 ± 650 – ca. 11,000	3	2	5	Cardich, 1987
11	Piedra Museo AEP-1 layer 6	12,890 ± 60–11,000 ± 50	3	4	7	Miotti et al., 1999; 2003
12	Tres Arroyos rockshelter	11,880 ± 250–10,280 ± 110	4	3	7	Massone, 2003
13	Cerro Tres Tetas cave	11,575 ± 140–10,260 ± 110	1	0	1	Paunero, 2000, 2003
14	Lago Sofia 1 cave	11,560 ± 70–10,300 ± 40	4	3	7	Martin, 2013
15	Milodón cave	11,330± *-10,200± *	1	2	3	Borrero and Martin, 2012
16	Cueva del Medio	11,120 ± 130–10,310 ± 70	5	3	8	Nami and Nakamura, 1995
17	Casa del Minero I cave	11,000 ± 55–10,970 ± 55	1	3	4	Paunero et al., 2007
18	Fell cave	11,000 ± 160–10,720 ± 300	5	3	8	Bird, 1988
19	Cerro Casa de Piedra 7 (CCP 7)	10,690± – 10,530 ± 620	1	1	2	De Nigris, 2004
20	La Gruta 1 cave	10,845 ± 61–10,400 ± 50	1	0	1	Franco et al., 2010
21	El Trébol rockshelter	10,600 ± 100–10, 570 ± 130	15	2	17	Hajduk et al., 2012
22	La María, Túnel cave	10,510± –10,400 ± 100	6	4	10	Paunero et al., 2007, 2010
23	AEP1- layer 4/5	10,470 ± 65–9230 ± 105	3	2	5	Miotti et al., 2003
24	Marifilo rockshelter 1	10,410 ± 70–8420 ± 40	2	0	2	Mera and García 2004
25	Epullán Grande cave	9970 ± 100–7550 ± 70	1	7	8	Cordero, 2011
26	Cuyín Manzano cave	9920 ± 240	3	0	3	Cordero, 2011
27	Chorrillo Malo-2	9740 ± 50–9690 ± 80	1	0	1	Franco and Borrero, 2003
28	Cerro Casa de Piedra 7 (CCP7) rockshelter	9730 ± 100–8300 ± 115	7	0	7	De Nigris, 2004
29	Marazzi rockshelter	9590 ± 210	1	1	2	Morello et al., 1999
30	Huenul cave unit IV	10,155 ± 98–9261 ± 66	2	0	2	Barberena et al., 2015
31	Baño Nuevo 1 cave	9530 ± 25–8530 ± 160	2	0	2	Mena et al., 2003
32	Maripe cave	9518 ± 64–7153 ± 50	3	0	3	Miotti et al., 2007, 2014
33	Los Toldos cave 3, layers 9 and 8	ca. 9500–8750 ± 480	5	2	7	Cardich, 1987
34	El Ceibo 7 rockshelter, layer 12	ca. 9500	5	1	6	Miotti and Salemmé, 1999
35	Traful 1 cave	9430 ± 230–9285 ± 105	1	0	1	Cordero, 2011
36	Arroyo Feo cave	9410 ± 70–8410 ± 70	8	0	8	Silveira, 1979
37	Cueva de Las Manos	9320 ± 90–9300 ± 90	7	0	7	Mengoni Goñalons and Silveira, 1976
38	Fell Cave	10,080 ± 160–9100 ± 70	1	0	1	Bird, 1988
39	La Mesada cave	9090 ± 40	2	0	2	Paunero et al., 2007
40	La Martita cave	8050 ± 90–7940 ± 260	2	0	2	Aguerre, 2003
41	El Verano cave	8960 ± 140–7500 ± 250	3	3	6	Durán, 1986/1987
42	Maripe cave, layer 4	88270 ± 87–8012 ± 80	2	2	2	Miotti et al., 2014
43	Las Buitreras cave layer VII	CA. 9000	1	2	3	Sanguinetti, 1976
44	Cerro Bombero	ca. 8850		1	1	Paunero, 2010
45	Fitz Roy	n/d	2		2	Carlini, pers. com.
46	Puerto Deseado	n/d	1		1	Carlini, pers. com.
47	Bahía Sanguineto (Lujanian stock)	n/d	x	x	x	Ameghino, 1880

Table 2
Frequencies of extinct and living mammals at archaeological sites in Pampa region.

#	Pampa sites in Fig. 1	¹⁴ C dating	Extinct	Living	N species	References
48	Arroyo Seco 2. Fauna	12,240 ± 110–11,190 ± 110	12	15	27	Politis et al., 2014
49	Arroyo Seco 2. Human occupation	11,320 ± 110–11,000 ± 100	10	13	23	Politis et al., 2014
50	Paso Otero 5	10,440 ± 100–10,210 ± 50	10	2	12	Martínez and Gutiérrez, 2011
51	Cerro La China	10,804 ± 75–10,525 ± 74	1	0	1	Mazzia, 2011
52	Tixi cave	10,375 ± 90–10,045 ± 95	2	13	15	Mazzanti and Quintana 2001
53	Los Pinos	10,465 ± 65–8750 ± 160	2	13	15	Mazzanti et al., 2013
54	Amalia site 2	10,425 ± 75	2	13	15	Martínez and Osterrieth, 2003
55	Cueva Burucuyá	10,000 ± 120	1	14	15	Mazzanti et al., 2013
56	Paso Otero 4	9283 ± 83–7314 ± 73	2	16	19	Álvarez et al., 2013
57	Campo Laborde	8090 ± 190–7750 ± 250	3	6	9	Politis and Messineo, 2008
58	Lobería 1 sitio 1	9878 ± 81	2	28	30	Mazzanti et al., 2013
59	Los Helechos	9640 ± 40	0	8	8	Mazzia, 2011
60	El Abra cave	9834 ± 65	1	14	15	Quintana et al., 2003
61	La Brava cave	9670 ± 120	0	9	9	Mazzanti, 1999
62	El Guanaco 1	9250 ± 40–7494 ± 74	3	6	9	Frontini, 2012
63	Arroyo Seco 2. Human burials	8980 ± 410–7043 ± 82	5	18	23	Politis et al., 2014
64	La Moderna	8356 ± 65–7448 ± 109	3	6	9	Politis and Gutiérrez 1998
65	El Guanaco 2	9140 ± 120–8123 ± 82	1	2	3	Frontini, 2012
66	Laguna de Los Pampas without human	8971 ± 77–8835 ± 83	3	7	10	Politis et al., 2012

(hairy and cingulates), and notoungulates emigrated to the North, (Cione et al., 2009).

Of the 12 Holarctic families (excluding Hominidae) which emigrated to South America from the limit Pliocene-Pleistocene, felids, ursids, camelids and equids (*Equus* and *Hippidion*), along with the South American native fauna, made up the Lujanian fauna that at the end of the Pleistocene was found by hunter-gatherer pioneers in Pampa and Patagonia. Of the 122 Lujanian species, only 16 have archeological record between both regions. On the other hand, if we only register those corresponding to mega mammals and large mammals, the use could have been much lower as regards selected species (Fig. 2).

Even though the biodiversity was greater during the period of late Pleistocene and early Holocene, when the first signals of human settlement in the south of South America were recorded (ca. 13 Ka BP), it was lower in Patagonia than that recorded in Pampa region (Miotti and Salemme, 1999).

Of the 14 extinct species of large mammals, 12 are Holarctic type and two are native from South America, of these, those corresponding to mega fauna were fully extinct (Alberdi et al., 1995; Cione et al., 2009, pp. 135). The biotic interchange did not produce an irreversible declination of biodiversity, which even increased in South America towards the end of Pleistocene, especially at the expense of the immigrants. Some mega mammals (glyptodonts) managed to survive the dramatic postglacial changes, until ca. of 7.5 Ka BP, date of the last appearance in Pampa region (Politis and Gutiérrez, 1998; Miotti and Salemme, 1999; Politis et al., 2004; Cione et al., 2015).

In this context, it is worth highlighting that if humans only hunted some of the mega and large mammal species of the Lujanian stock, this action did not cause the extinction firsthand, but rather a kind of chain reaction in the highly unstable ecosystems of the end of Pleistocene, which were producing a numerical reduction of these animal populations. In that sense, the numerical decline of large and mega mammals that had already been subjected to re-accommodation due to profound postglacial environmental changes was accelerated by human presence since the selective hunting managed to break the weakened food chains, and this way favored the eventual extinction of different species. In this respect, it cannot be established a sequence of extinctions between mega, large and small mammals due to the focus of human interest for certain preys. These hunts, when reducing selectively some populations of mega and large mammals, managed to break the ecological balance between faunas and their environments, being therefore an extremely disturbing factor in the latter. An example of

this is the case of guanacos that were, both in Pampa and in Patagonia, the species mostly used by hunter-gatherers, and they have reached the present time, in spite of the fact that hunting was sustained by humans in both regions throughout all Holocene.

4. Zooarchaeological database

All archeological sites with accurate chronological and taxonomic information about the presence of Lujanian fauna species were considered for this work. Moreover, the paleontological information whose temporal dispersion coincides, at least in part, with the human presence in both regions was also taken into account. In some cases, they are penne contemporary and in others, the taxa date is available specifying even more the presence of determined taxa in an area. Thus, we analyzed 18 sets for Pampa region and 44 sets for Patagonia, having both present and extinct fauna and with taxa of large and mega mammals. Also, those taxa of medium mammals were taken into account, but only the presence/absence of those of small and micro mammals was reported since their information is very heterogeneous in the publications. Tables 1a and 1b, 2 and 3 show these data summarized and the other taxa recorded in Pampa and Patagonia sites. These data are considered indispensable for the analysis of biodiversity and fauna use in different environments of both regions.

5. Zooarchaeological results

The results of the relative taxonomic abundance expressed in Ntaxa obtained for both regions have resulted from the quantitative analyses of each site (Tables 1–4; Figs. 3 and 4).

In all sites of both regions, the common factor is the *Lama guanicoe* species, which, as it was seen above, it is characterized by the high environmental adaptability, even in very eremic conditions. On the other hand, it is the species that even today inhabits in some sectors of the south and west portion of Pampa region and all Patagonian region, and exceeding its geographic dispersion, reaches the Andean territories of Argentina, Chile and Peru, and the Bolivian plateau. The zooarchaeological remains indicate a high level of human consumption in both regions, moreover, its gregarious ethology and the preference for open steppe environments, together with the associated weapons in the archeological sites, allow inferring that these camelids were the favourite preys of the first hunter-gatherers, even until the post-Hispanic times (Borrero, 1990; Miotti, 1998; Mengoni Goñalons, 1999; Miotti and Salemme, 1999, 2004; Politis and Madrid, 2001; Miotti, 2012; Salemme and Miotti, 2008; among others).

We found out that in the time period previous to 12.6 Ka BP only archeological sites with Pleistocene fauna were recorded in Patagonia (Tables 1a, 1b, and 2), and only after that date, these taxa appeared represented in archeological sites of both regions, what indicates an older record of human-Pleistocene fauna co-existence for the Patagonian region. The only exception in Pampa corresponds to the archaeological site Arroyo Seco 2, which seems to

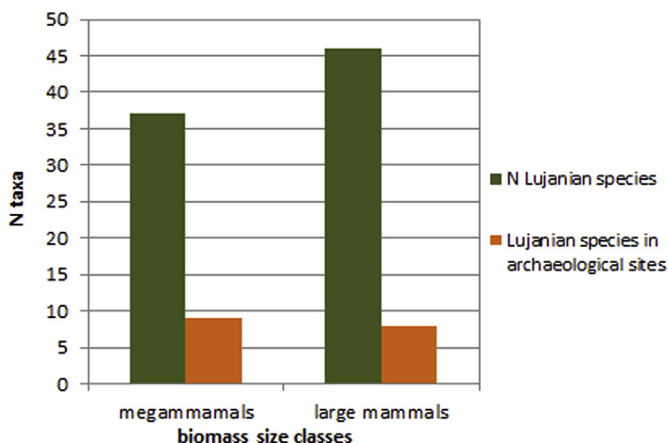


Fig. 2. Biodiversity estimated in Lujanian taxa.

Table 3
Temporal and regional faunal distributions.

Regions N taxa Intervals	Patagonia			Pampa		
	Extinct	Living	N sites	Extict	Living	N sites
13.5–12.5 Ka BP	8	5	8	0	0	0
12.5–11 Ka BP	8	4	11	17	12	2
11–9.5 Ka BP	5	18	15	6	28	12
9.5–7.5 Ka BP	2	12	10	4	23	5
Total N sites	22	38	44	27	63	19

Table 4
Species with archaeological record.

Code	Taxa	Patagonia	Pampa
1	Gastropods	x	x
2	Volutidae (marine snail)	x	x
3	<i>Aulacomya ater</i>	x	
4	<i>Amiantis</i> sp.		x
5	<i>Adelomelon brasiliensis</i>	x	x
6	Fishes	x	x
7	<i>Anura and ophidia</i>		x
8	Ave	x	x
9	<i>Polyborus</i> sp	x	
10	<i>Phonicopterus ruber</i>		x
11	Rheidae	x	x
12	<i>Rhea americana</i>	x	x
13	<i>Pterocnemia pennata</i>	x	
14	<i>Eudrommia elegans</i>	x	x
15	<i>Nothura maculosa</i>		x
16	<i>Fulica</i> sp.		x
17	<i>Speotyto cunicularia</i>		x
Mammals			
18*	<i>Scelidotherium</i> †	x	x
19	<i>Myiodon darwini/ listai</i> †	x	x
20	<i>Megatherium americanum</i> †		x
21	<i>Lestodon armatus</i>		x
22	<i>Glossotherium</i> sp.†		x
23	<i>Eutatus seguini</i> †		x
24	<i>Glyptodon</i> sp.†		x
25	<i>Panochthus</i> sp †	x	
26	<i>Doedieurus</i> sp.†		x
27	<i>Sclerocalyptus</i> †		x
28	<i>Tolypeutes</i>		x
29	<i>Choetophractus villosus</i>		x
30	<i>Zaedyus pichiy</i>	x	x
31	<i>Dasyypus hybridus</i>		x
32	<i>Holochilus brasiliensis</i>		x
33	<i>Dolichottis patagonum</i>		x
34	<i>Lagostomus maximus</i>		x
35	<i>Myocastor coypus</i>		x
36	<i>Lagidium</i> sp.	x	x
37	<i>Pantera onca</i> †	x	
38	<i>Conepatus</i> sp	x	
39	<i>Lutreolina cassicaudata</i>		x
40	<i>Felis</i> sp.	x	x
41	<i>Smilodon</i> sp †	x	
42	<i>Felis concolor</i>	x	x
43	<i>Lynchaillorhis colo-colo</i>	x	
44	<i>Lontra</i> sp.	x	
45	<i>Arctotherium tarijense</i> †	x	
46	<i>Canis</i> sp	x	x
47	<i>Canis (D.) avus</i> †	x	x
48	<i>Canis (D.) culpaeus</i>	x	x
49	<i>Lyncodon patagonicus</i>	x	x
50	<i>Macrauchenia patachonica</i> †	x	x
51	<i>Palaeolama wedelli</i> †	x	
52	<i>Toxodon</i> sp.†		x
53	<i>Cuveronius</i> sp†	x	
54	<i>Equus (amerhippus) neogaeus</i> †		x
55	<i>Hippidion saldiassi</i> †	x	x
56	<i>Tayassu</i> sp.		x
57	<i>Lama</i> sp	x	x
58	<i>Lama (V.) gracilis</i> †	x	x
59	<i>Lama guanicoe</i>	x	x
60	<i>Hemiauchenia paradoxa</i> †	x	x
61	<i>Ozotoceros bezoarticus</i>		x
62	<i>Hippocamelus bisulcus</i>	x	
63	<i>Pudu pudu</i>	x	
	<i>Homo sapiens</i>	x	x
	N taxa	38	48

† extinct species megamammal large mammal medium and small size fauna

N°18*, *Scelidotherium* includes remains of one young individual assigned to *Diabolotherium* cf. *nordenskioldi*, Which and is related to *Scelidotherium*.

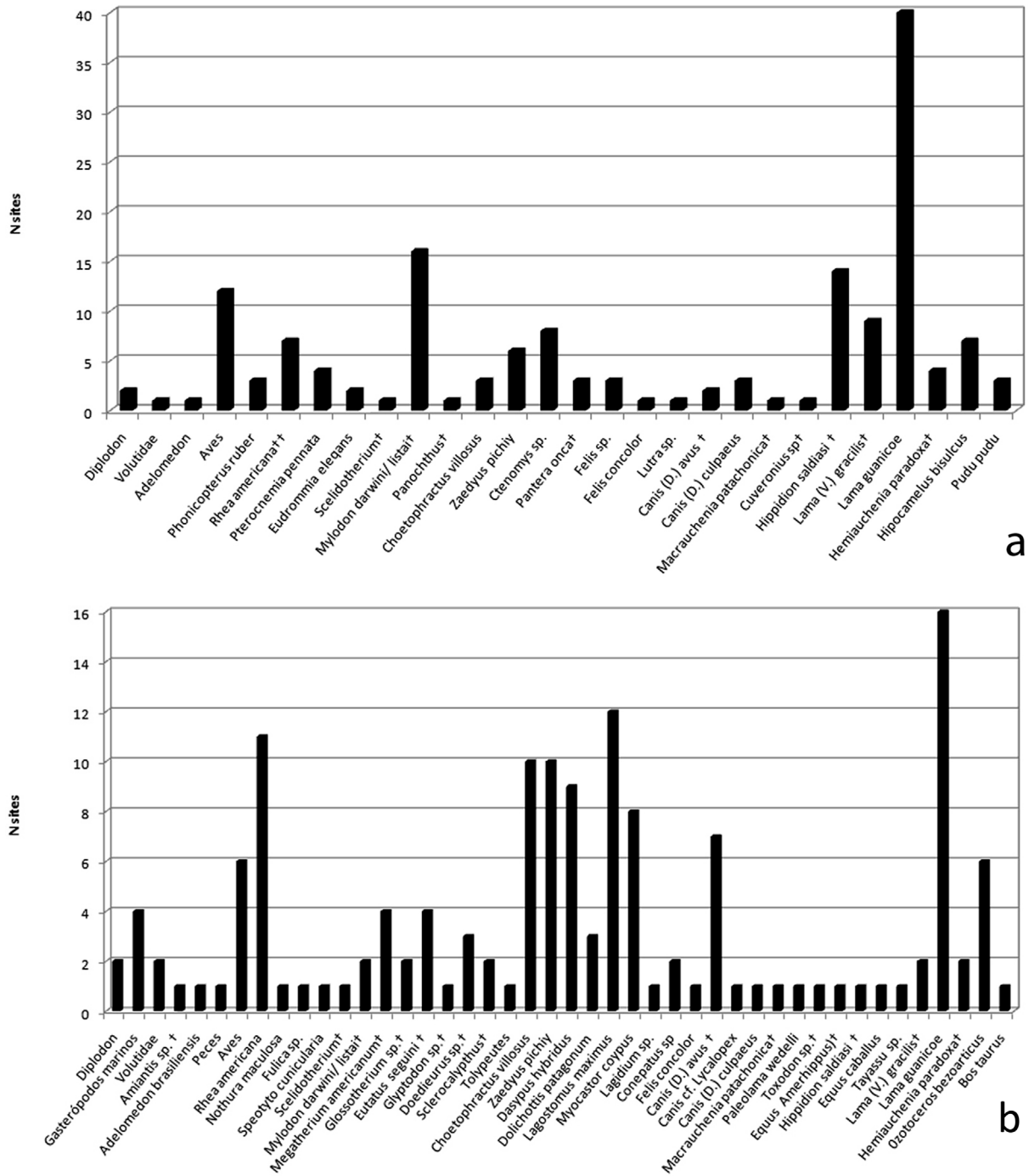


Fig. 3. Taxonomic frequency in a) Patagonia, and b) Pampa. † extinct species. †† disappear in the region.

meet this condition of presenting a high number of mega and large mammal species for 12,600–12,000 RYBP. Nevertheless, the detailed information obtained from the taphonomic analyses indicate that for the inferior levels of the site, humans only hunted/used few of all the taxa present in the area (Politis, 2014). On the other hand, even though the spatial distribution of faunas with Lujanian elements is greater in Patagonia than in Pampa, the latter presents a greater taxonomic diversity (Tables 1 a-b, 2 and 3 and Figs. 2 and 5).

6. Characteristics of the species with archaeological record

The species that we consider as key in this work correspond to the association of Lujanian mammals corresponding to the Biozone of *Equus (A) neogaeus* Association, according to Cione et al. (2009), since these are the ones that had better chances of having coexisted a longer time with the first humans, and therefore, having being exploited by the hunter-gatherers that colonized both regions of South America (Fig. 5).



Fig. 4. Taxonomic abundance (living and extinct mammals) in a) Patagonia and b) Pampa sites.

Regarding the *Xenarthra* group, several findings can be mentioned in Southern Patagonia, though not always its association with archaeological sites is related with mylodonts. However, in 2007, in Fitz Roy locality (#45), Santa Cruz province, during the excavations for a sport building, remains of (*Panochthus*), and

others referred to *Scelidotherium* (A. Carlini, com. pers.) were found. Both taxa form part of the Lujanian fauna (late Pleistocene) and, so far, they have not been documented in sites of the Patagonian region, since only accuracy ascribed those of Bahia Sanguineto (#47) and Puerto Deseado (#46) to Lujanian xenarthrans remains (Tonni

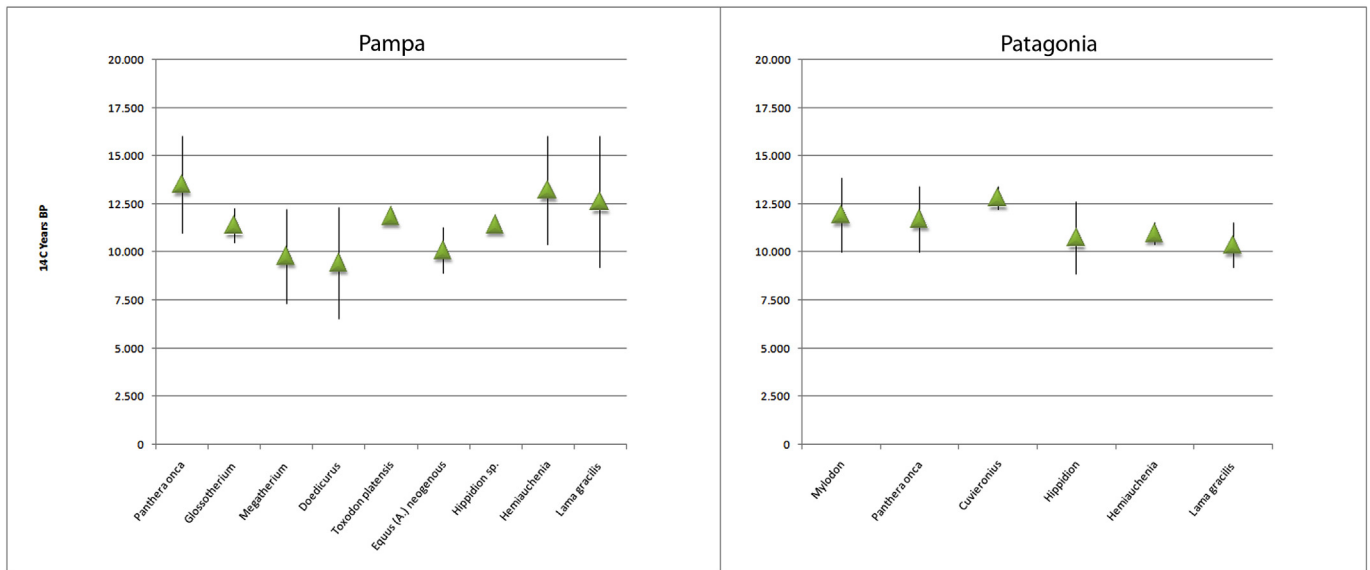


Fig. 5. Date of first and last appearance of species of Lujanian fauna in both regions. a) Patagonia y b) Pampa.

and Carlini, 2008). Such mammals appear stratigraphically in sediments of lagoon and swamp type, as well as wind type, and their habitats were those of open savanna and grasslands related to periglacial areas and with temperatures lower than today. In both regions these basic ecological characteristics for Lujanian mammals were confirmed by independent evidence lines such as palynology, the studies of sea cores, and stable isotopes (Czerwonogora et al., 2011).

7. Dates of the first and last appearance of extinct taxa

The results of taxa dates obtained in archaeological sites of Pampa and Patagonia allow supporting the hypothesis that Pleistocene large and mega mammals had a period of coexistence with humans of ca. 5000 years (Cione et al., 2009). However, the coexistence times between humans and mega fauna were different in the different species, in both regions. In Fig. 5 it is shown this situation based on the zooarchaeological information of each region.

This analysis together with the zooarchaeological information of the previous paragraph allows suggesting that hairy Xenarthra (sloths) and Cingulates (glyptodonts) had greater possibilities of becoming prey for humans in Pampa region. This difference is based on the fact that, in Pampa region, the Cingulates disappeared by mid-Holocene, ca. 7.5 Ka BP (Politis and Gutiérrez, 1998; Gutiérrez et al., 2010), while in Patagonia the last records correspond to the end of the transition Pleistocene/Holocene, i.e., ca. 10 Ka BP (Borrero and Martín, 2012; Marchionni and Vázquez, 2012; Miotti and Marchionni, 2012; Martín, 2013) (Fig. 5). This may suggest that the potentiality of these animals as resource for human consumption was extended 2500 years more in Pampa than in Patagonia. On the other hand, their most abundant use in the former region is supported by the vast evidence of primary butchering and consumption marks, and the greatest taxonomic richness per taxon (Table 4 and Fig. 3).

In Patagonia there are no records of glyptodont remains in archaeological sites (Table 4 and Fig. 3) but there have been numerous findings of giant sloths; though in very few of these findings there is clear evidence of butchering marks and anthropic burnt (Borrero et al., 1997; Miotti and Cattáneo, 2003; Hajduk et al., 2009, 2012; Lezcano et al., 2010; Marchionni and Vázquez, 2012; Marchionni, 2013; Miotti and Marchionni, 2012, 2014). However, in

this region the number of archaeofauna elements is overdimensioned since the most represented parts in almost all the Patagonian sites correspond to dermal bones and in some cases, like in the Milodón Cave and Baño Nuevo-1 cave (Fig. 1), to leather fragments with little bones included. This evidence of several dermal bones is a key marker for being able to interpret these findings in function of the human choice regarding the use of sloths. This recurrent data in different Patagonian caves encouraged the hypothesis of an initial cave occupation by animals, and then, a subsequent use by humans. In this case, there may be a temporal difference between the megafauna occupation and humans. The taphonomic and stratigraphic studies indicate natural death of animals and previous to peoples at caves (Mena and Reyes, 2001; Borrero and Martín, 2012). In others caves, like Huenul 1, Milodón, Los Chingues, the first stratigraphic levels contain milodont's dungs. However, in some cases like in El Trebol cave (Fig. 1 #21) signals of use of mylodonts are clearer. The excavators inferring that mylodonts were used by humans: "Algunos huesos dérmicos presentan una pátina negro brillante, indicando que fueron expuestos al fuego cuando aún conservaban restos de tejido blando." (Hajduk et al., 2009, pp. 959, pp. 959) ... "El rasgo más destacable en estos huesos dérmicos (Mylodontinae) es la presencia de claras huellas de corte producidas por el hombre, en algunos casos profundas y reiteradas." (Hajduk et al., 2009, pp. 960). The hypothesis of the use of dead animal leather and meat should not be discarded by the arguments further discussed.

The presence of notoungulates is very scarce in the analyzed archaeological sites, being absent in the Patagonian record, while, in Pampa region their presence is exclusively in Arroyo Seco 2 site only, with the species *Toxodon platensis* (Politis et al., 2014; Salemme, 2014). It is observed that this evidence may only support the hypothesis of coexistence between humans and such species since the record corresponds to a single carpal, which is dated $11,750 \pm 70$ (CAMS16839) ^{14}C BP and does not present evidence of human action. However, this information together with the taxon dates of the site (Politis, 2014) indicate low chances that the species had coexisted during a long time with the first settlers of the area, therefore it seems parsimonious to keep the hypothesis of coexistence with the humans for a short time, but we do not believe that this species could have form part of the group of resources chosen by humans for consumption. This reasoning may explain partly the

low archaeological representation of the species at Pampean regional level, since this is indeed frequent in paleontological groups of the end of Pleistocene.

Horses have a higher numerical representation in Patagonian contexts than in Pampa ones (Fig. 3), being their last appearance date 2000 years earlier in Pampa than in Patagonia (Fig. 5). Their longer coexistence period with humans in Patagonia could have been an important cause for having been more intensely used in this region. However, there are other archaeological markers that allow inferring a more intense use of equids by hunter-gatherers in Patagonia. Among these markers, there are equid images recorded in rock art from Los Toldos, La María and Piedra Museo sites (Cardich, 1987; Miotti, 1991, 1993–96; Miotti et al., 2007; Miotti and Carden, 2007; Paunero et al., 2007; Carden, 2009), most of the anatomic units, of different age categories, and abundant and clear cut/blow marks of butchering for the species *Hippidion saldiasi* in several Patagonian sites support the hypothesis about economic use of these mammals.

On the other hand, it is worth highlighting that in Patagonia there is only one species recorded, *Hippidion saldiasi*, while in Pampa the equids were represented by two species, *Hippidion* sp. (probably *H. principale*) and *Equus (Amerhippus) neogaeus*, though these are recorded in an only archaeological site, Arroyo Seco 2 (AS2). Even though in recent works, the archaeologists consider that in Pampa region both species were available, only *Equus* is the species with evidence of human use (Gutiérrez and Johnson, 2014; Salemme, 2014). These marks of cut and fracture impact are still scarce and they were recorded in a bone (radius) of those recovered in the only archaeological site where the species appeared represented (Gutiérrez and Johnson, 2014, pp. 124; Salemme, 2014, Table 4.8).

In Patagonia *Hippidion saldiasi* was recorded in fourteen localities: Los Toldos 2 and 3, Piedra Museo AEP-1, La María, Túnel cave, Casa del Minero 1, Cave 6 from El Ceibo, Lago Sofía 1 and 4; Fell, Pali Aike, Cueva del Medio, Los Chingues cave, Del Puma cave, and Tres Arroyos rockshelter, being the representation of anatomic units numerous in each site, generally corresponding to individuals of different age groups and presenting clear marks of prey processing. In this region, the time of the last equid appearance reached the early Holocene, around 8.5 Ka BP, recorded with taxon date in cerro Bombero site (Paunero, 2010). This evidence, combined with the gregarious nature of these mammals, an ethology similar to that of camelids, which undoubtedly were the most important preys in both regions, allows stating that the coexistence with equids may have been another factor contributing to adjust this species with the programmed hunting strategies of the first inhabitants in the Patagonian region. In such sense, horses are considered a selected resource searched by the first settlers of the southern extreme, and in Patagonia, they might have been very interesting in the economic, social and symbolic spheres. Probably, we should expect new evidence for supporting that a similar use of equids took place among hunter-gatherers in Pampa region.

In both regions, the species with more possibilities of having been important prey for humans is the camelids (Figs. 3 and 4), and within them the guanacos, which are considered main resources for hunter-gatherers until late Holocene. The abundance of remains of these mammals in most sites of both regions, along with the fact that their presence continues nowadays, supports such hypothesis. This record that leads to a strategy of hunting specialization during mid Holocene (Miotti and Salemme, 1999; Miotti, 2012, and references therein) is now outlined as a trend in hunting strategies which may have started at the beginning of human occupation.

As regards other extinct camelids, present in the first settlements in both regions, they also have a different representation. While *Hemiauchenia paradoxa* and *Lama gracilis* have an ephemeral

evidence in Pampa region, with presence only in site AS 2, their record in Patagonia is much higher in number of sites and in amount of anatomic parts, as well as in amount of cut and chop traces (Nami and Menegaz, 1991; Miotti, 1998; Miotti and Salemme, 2005; Miotti and Marchionni, 2012; Martin, 2013). In this case, it can also be interpreted that the longest date of the last appearance in Patagonian sites (ca. 9.2 ka BP), together with an ethology similar to that of guanacos, may have contributed to the greatest and longest consumption of these mammals in the most southern region.

The large carnivores, such as the *Panthera onça*, have a very low archaeological representation in sites of Patagonia (Fig. 5) and null in those of Pampa. However, this species that nowadays lives in rain forests as far as the North of Argentina, inhabited both regions towards the end of Pleistocene. In Patagonia, the time of coexistence with humans was of 2000 years (Fig. 5), being ca. 10 ka BP the last records of the subspecies *Panthera onça mesembrina*. In Pampa *Panthera onça* inhabited until the beginning of the 20th century, but there are no archaeological records of the use given to this species by the first settlers in this region. This unequal archaeological evidence in both regions brings into questions the different use of these large felines by humans (Table 6). Taking into account that in Pampa the time of coexistence was much longer, the most parsimonious hypothesis is that the Pampean hunter-gatherers had not used jaguars as economic, social or symbolic resource (Table 6). On the contrary, and although a short period of coexistence was recorded in Patagonia, the archaeological evidence indicates that these animals formed part of, at least, the social and symbolic spheres of the first humans (Table 6). The sites where teeth of this species were recorded are Cueva del Medio, La María and El Ceibo. In this last Locality it was also documented a very big painting, assigned to that feline (Cardich, 1987; Miotti and Carden, 2007). This form of appropriation of one of the extinct species corresponding to a large carnivore, which at the same time was predator of Pleistocene large and mega mammals, is, in every sense, assignable to the symbolic category. This interpretation considers that the evidence of their remains associated to the first archaeological contexts is related with large images, outstanding on painting panels as well as with the appropriation of tusks and paws. This information supports the hypothesis of image appropriation or of parts of these large carnivores as elements that even today are considered mimetic of super natural power in several societies (González, 1974; Reichel-Dolmatoff, 1975; Dillehay and Kaulick, 1984–85; Ingold, 1986; Taçon et al., 1996; Politis and Saunders, 2002; Miotti and Carden, 2007), and in that sense, that those items might have been considered as metonymic and/or metaphoric of prestige and/or power among the first Patagonian explorers. However, such evidence is not enough for formulating the incidence in hunting for an economic use. In numerous societies, from hunter-gatherers to agricultural or pastoral, the jaguar image as power symbol and social belonging has been important until today, in ceremonies, artifacts, artistic representations, legends and other narratives as well (see references above).

8. Discussion

The zooarchaeological, ethological, coeval information between humans and Pleistocenic extinct fauna presented here supports the hypothesis of Broken Zig Zag (see, Cione et al., 2009, 2015, and citations therein) as a varied and complex set of environmental and cultural factors of mammal extinction. In this frame, the amount of taxa of extinct fauna appearing in archaeological sites of first colonization in both regions does not exceed the 30% of the total (Fig. 2), therefore they are few as regards those of living species in Holocene which were used, firstly, as product of human hunting. As

Table 5
Ecological and ethological characteristics of extinct Pleistocene mammals with archaeological record.

Lujanian Species	behavior	Activity	feeding habits	Potential depredators	environment	climate
<i>Panthera onça</i>	lonely	crepuscular/ dusk	carnivore	unknown	Forest/moist Savanna	tropical/ temperate
<i>Smilodon Sp</i>	lonely	diurnal	carnivore	without	Savanna	cool temperate
<i>Arctotherium tarijense</i>	lonely	diurnal/ daytime?	omnivore	without	?	cool temperate
<i>Canis (D) avus</i>	lonely	diurnal/ dusk	omnivore	unknown	Savanna/steppe?	cool temperate
<i>Scelidotherium Sp</i>	?	diurnal/ daytime	?	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Lestodon armatus</i>	?	diurnal/ daytime	?	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Mylodon darwini/listai</i>	?	diurnal/ daytime	grazer	grand carnivores/ human	open shrub steppe	cool temperate
<i>Megatherium Sp</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Glossotherium Sp.</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Eutatus seguini</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Gliptodon Sp</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Panochthus Sp</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Doedicurus Sp</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Savanna/grassland	cool temperate
<i>Sclerocalyphus Sp</i>	lonely?	diurnal/ daytime	grazer	grand carnivores/ human	Grassland/schubby	cool temperate
<i>Toxodon Sp</i>	herd?	diurnal/ daytime	grazer	grand carnivores/ human	wetland?	cool temperate
<i>Macrauchenia Sp</i>	herd?	diurnal/ daytime	grazer	grand carnivores/ human	Grassland/schubby	cool temperate
<i>Gomphoteriidae</i>	herd	diurnal/ daytime	grazer	grand carnivores/ human	Grassland/woodland	cool temperate
<i>Hippidion saldiasi</i>	herd	diurnal/ daytime	grazer	grand carnivores/human	Plains and mountain	cool and wet
<i>Equus (A.) neogaeus</i>	herd	diurnal/ daytime	grazer	grand carnivores/ human	Plains and mountain	cool temperate
<i>Hemiauchenia paradoxa</i>	herd?	diurnal/ daytime	grazer	grand carnivores/ human	Grassland/schubby	cool temperate
<i>Lama gracilis</i>	herd	diurnal/ daytime	grazer	grand carnivores/ human	grassland, schubby	cool temperate
<i>Lama guanicoe</i>	herd	diurnal/ daytime	grazer	grand carnivores/ human	Grassland/schubby steppe	cool temperate
<i>Ozotoceros bezoarticus</i>	herd	diurnal/ daytime	grazer	grand carnivores/ human	Grassland plains	tropical/ temperate

Table 6
Different human uses of mammalian fauna in Pampa and Patagonia regions.

Regions	Pampa			Patagonia		
	Economic	Social	Symbolic	Economic	Social	Symbolic
Use of Taxa						
Xenarthrans	yes	yes	yes	yes	yes	yes
Equids	yes	n/d	n/d	yes	yes	yes
Camelids	yes	yes	n/d	yes	yes	yes
Grand Carnivores	No Data			No	yes	yes

a consequence, even though it is observed that the glyptodonts lasted until mid Holocene for Pampa region (ca. 7 ka BP), in Patagonia, their disappearance was completed 3000 years before. However, we can suggest that in Patagonia the social and symbolic use of some extinct species may have indeed survived among hunter-gatherers until the end of Mid Holocene.

Thus, it is inferred that from the end of the Pleistocene to mid Holocene, biodiversity trends, both in Pampa in Patagonia, were decreasing with some variables in both regions (Fig. 6). The greatest

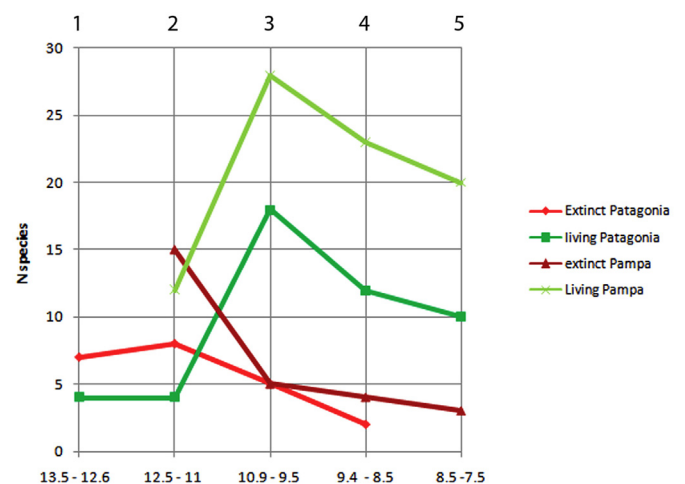


Fig. 6. Faunal diversity in Pampa and Patagonia: temporal trends. 1 to 5 are temporal intervals expressed in ka BP.

mammal biodiversity recorded archaeologically at the end of Pleistocene or beginning of Holocene was due to the presence of mega and large mammals of Lujanian stock, which decreases in sites of both regions towards the second interval of human occupation, ca. 11.5 Ka BP (Fig. 6) because of the extinction process both of mega and large mammals. From that date, the inversion in diversity trends took place in both regions, between the extinct and present species. The variety of extinct species decreased abruptly and the representation of large living mammals increased. Even though the mostly used species was the guanaco in both regions from the beginning of the first settlers, the complementary resources changed, being the cervids which complemented the economic resources in Pampa and north Patagonia, while in Patagonia the specificity about guanacos was more significant (Fig. 4).

In Pampa, the first records of the Pleistocene fauna use in archaeological sites were later than in Patagonia, which indicates that the interaction (humans-extinct fauna) began roughly 1000 years earlier in Patagonian sites than in Pampa sites. The use of Pleistocene fauna continued increasing in both regions during the third interval (10.9–9.5 Ka BP) and fourth interval (9.4–8.5 Ka BP), reaching the fifth interval (8.4–7.5 Ka BP) only with present fauna in both regions and the survival of cingulated xenarthrans only in Pampa region until 7 Ka BP (Fig. 6). Xenarthra disappeared 1000 years before in Patagonia ca. 8.5 Ka. BP, when in that region the extinction of all Pleistocene species was completed. Nevertheless, in Pampa, survival of some glyptodonts in environmental shelters of that region reached ca. 7 Ka BP.

Another peculiarity, in both regions after 8.5 Ka. BP, is the most diverse use of taxa of both large and small mammals in Pampa region, while in Patagonia the almost exclusive resource was represented in the species *Lama guanicoe*, which was joined, as a complement, by some cervids in the Andean sector and pinnipedes on the Atlantic coast. The reduction in biodiversity in archaeological sites may have resulted from the extinction process. An outstanding issue of the fauna variations of both regions is that in Patagonia the taxonomic diversity was always below that recorded in Pampa region (Fig. 6). Despite this difference of a greater mammal variety in Pampa region than in Patagonia, in both regions the guanaco dominated all archaeological contexts before and after the great extinction of Pleistocene species. This supports the hypothesis of a greater adaptation between hunters and preys, positioning the guanaco as the main resource from the beginning of colonization. On the other hand, even with a wider biodiversity in Pampa than in Patagonia, the use of fauna was of larger spectrum in the human occupations of both regions until the third interval (Fig. 6), though with main contributions obtained from guanacos.

As regards the change of strategies of fauna appropriation, we observe that towards 10 Ka BP the greatest biodiversity increment took place in both regions dominated by present faunas (Figs. 4–6). The contexts of hunting technology and zooarchaeological, until then, indicate that the prevailing strategy may have been the wide generalized hunting, though with a prevalence of large mammals such as guanacos. In both regions, the gregarious animals, such as the camelids and equids in Patagonia, and the camelids, equids and cervids in Pampa, seem to have been predominantly sought by humans as economic resources. However, in all sites, the anatomic richness and the richness of use and consumption evidence was always focused on guanacos. After 8.5 Ka BP, the strategy in both regions changed, turning to a greater speciation on guanaco hunting (Miotti and Salemme, 1999; Miotti, 2012). Therefore, the change in strategy that in previous works (Miotti and Salemme, 1999) we placed between early Holocene and Mid Holocene, with the new regional information we are able to place it around 9.5 Ka BP, at the end of the third interval (Fig. 6).

In this sense, the hypothesis, which assigns the first humans a

catalyst role in the process of megafauna extinction in South America, is still the most parsimonious (Cione et al., 2009, 2015). Even though, since the earliest peopling humans had used species of extinct and living Pleistocene mammals, the archaeological evidence presented herein for both regions indicates that humans were not the main responsible for the extinction by mass slaughter but rather another factor which destabilized the environments already in crisis about 3000 years before the human arrival in South America. The human settling in a new environment produces changes in the ecosystems from their interaction. The interaction in those finipleistocene environments where deep climatic and environmental changes had been taking place (Mc Culloch et al., 2000; Rabassa, 2008) produced the final disarticulation of trophic chains with differential extinction structures in different mammal species, and such species did not manage to overcome population decreases which repeatedly occurred before the human arrival in the continent (Cione et al., 2015).

Particular cases for both regions are those of giant sloths, glyptodonts and large carnivores such as jaguars. In Patagonia these mammal groups lived with humans around 2500 years (Fig. 5), however, the archaeological evidence suggests an opportunist use of giant sloths and jaguars, while the glyptodonts were only recorded in paleontological sites (No 45, 46 and 47 of Tables 1 and 2, and Fig. 1), and consequently, the appropriation of all these animals might have influenced more significantly the social and symbolic spheres than those economic. That is, they were used for learning about the new places and their beings but they were not focus of hunting strategies for satisfying their basic needs (food).

In Pampa, both groups lived longer with humans (Fig. 3), however, the same as in Patagonia, giant sloths acquired an opportunist appropriation, while it is impossible by now to assign any kind of human use of jaguars. This importance was reverted in this Pampean region in the case of glyptodonts (xenarthrans cingulates), from which there is clear evidence of economic (Álvarez et al., 2013; Politis et al., 2014; Salemme, 2014; Martínez et al., 2016), but is weakness of social and symbolic use (Table 6).

The discussion about anthropological, archaeological and palaeoecological information allowed us to state that the knowledge about them lasted in the social imaginary, even after their extinction, through rock art, in curated and/or claimed artifacts, such as scutes, paws and teeth, present in some Pampean and Patagonian contexts. This materiality of the extinguished fauna may also be indicating that these animals had their social importance in the narratives of stories of places and people, possibly in ceremonies, myths and legends.

For horses (*Equus* [A.] and *Hippidion*) and camelids (*Lama guanicoe* and *Lama gracilis*), all of them herd mammals of grazing and running habits (Table 5), the archaeological and ethnographic evidence indicates a human appropriation through ambush and planned hunting. We can add the pattern of selected places for such practice. Both in Pampa and Patagonia, these places coincide with special sectors and lagoon and/or river banks for specific activities such as hunting and prey processing. Among the most outstanding sites we can mention Paso Otero 4 and 5, Campo Laborde, Cerro El Sombrero, Cerro Amigo Oeste, Piedra Museo, where the recurrence of these microenvironments working as fauna trappers and as topographic traps for lurking and capturing preys are present. Moreover, in both regions there are lithic contexts of projectiles such as spears FTP and triangular of straight base are added to these sites (Nami and Menegaz, 1991; Miotti et al., 1999; Mazzanti and Quintana, 2001; Massone, 2004; Messineo et al., 2009; Flegenheimer et al., 2013; Martínez and Gutiérrez, 2015; Miotti and Terranova, 2015). This evidence is consistent and reliable and suggests that the equid and camelid appropriation is related with strategies of programmed hunting. These strategies may have been

by ambush and use of special conditions of some continental aquatic landscapes, found only in some sectors of lagoons and streams, where small elevations present in the surroundings could have allowed concealment of the hunters (see works cited above). This argument has a similar pattern as regards the use of landscapes, mammal fauna and strategies of collective hunting between hunter-gatherer societies from different parts of America, from the end of Pleistocene to the end of the 20th century (Speth, 1983; Frison and Todd, 1987; Binford, 1991; Miotti, 1993–96; Miotti et al., 1999, 2004; Martínez, 1999, among others).

However, equids of both species have a lower hunting incidence in Pampean region than in Patagonia. In this last region *Hippidion* appears represented in numerous sites, being also more numerous and clearer the evidence of chopping and human consumption than in Pampean sites (Miotti and Cattáneo, 2003; Miotti and Salemme, 2005; Marchionni, 2013).

Possibly, as equids are gregarious animals, of open environments and share these with camelids, the hunting strategy of both could have been adjusted well to technology, using the same weapons and lurking forms for their capture. Moreover, in Southern Patagonia it is remarkable that zoomorphic images assigned to horses were represented in several sites such as Cave 6 of Los Toldos, Cave Túnel I of La María and possibly their tracks may have been recorded in the petroglyph of Piedra Museo. In this last case, even though their chronological order is discussed (see Carden, 2009 and reference therein) due to the fact that the petroglyphs lean on the stratigraphic layer corresponding to ca. 7.7–7.4 years BP (Miotti et al., 2003), the social use of equids is brought into question even for times when equids had already disappeared in both regions. In this case, the persistence of extinct animals in social memory would be similar to that previously referred to for xenarthrans. Thus, the symbolic use of that fauna through collective memory of societies could have moved at least 1000 years the idea of Pleistocenic horses that lived in Patagonian steppes. The last appearance in the Patagonian environment was recorded in 8.5 Ka BP, in the paleontological site Cerro Bombero, in Santa Cruz central plateau (Paunero, 2010).

This form of narrative and transmission, from generation to generation, of the knowledge of environments and beings who were extinct when being materialized in rock art or in ornaments/offerings, is a symbolic narrative that the ancient settlers may have used for transmitting to their descendants the history of the ancestors who colonized that place with different characteristics and beings from those they knew (Politis and Saunders, 2002; Rockman, 2003; Miotti and Carden, 2007; Miotti et al., 2015). When the scale of information about extinguished or mythic beings and landscapes lasts in wide regions and can be resignified by centuries and millenniums in societies, such as the case of the appropriation of many supernatural and/or natural beings (unicorns, dragons, jaguars), it is then when this is considered as social knowledge and culturally learned (Ingold, 1986; Taçon et al., 1996; Saunders, 1998; Meltzer, 2003).

The evidence of few cut marks in anatomic units of mylodonts is present in few sites, AEP1, El Trébol, Paso Otero 5, and AS 2, remaining as a low signal for supporting the hypothesis of a systematic hunting of these animals. That is why it is more parsimonious to hold the hypothesis of opportunist use (Borrero and Martín, 2012) of any dead animal by non human reasons, and the subsequent attainment of their parts, not for food, but for diverse uses like bones for fuel (Álvarez et al., 2013); or leather. It is significant that in Baño Nuevo-1 cave, dermal bones (osteoderms) could have been associated to the death treatment with the human body wrapping. However, taphonomic and stratigraphic investigations indicate that these bones are not associated to cultural layers (Mena and Reyes, 2001). Similar cases are Fell and Pali Aike,

where charred/burnt human remains were covered by large Mylodont bones (Hyslop, 1988). Third similar case and associated to human burials is that of AS2, in Pampa (Salemme, 2014). In these contexts, though, bones do not present cut or human action traces. Meanwhile in El Trébol cave, osteoderms appear burnt and show bearing anthropic cutmarks (Hajduk et al., 2009, 2012; Lezcano et al., 2010). This evidence reinforces the idea that their association to the use of leather by human would be a hypothesis to evaluate.

From the paleontological information of these three sites of the central plateau, it can be inferred that Lujanian stock of xenarthrans, horses and camelids, placed in Bahía Sanguineto (Ameghino, 1880), together with those from Fitz Roy, Puerto Deseado and the only horse individual found in Cerro Bombero, may have been available for the late Pleistocene in the plateau. This information added to that paleo-environmental of the area, mainly palinological (Borromei, 2003; Mancini et al., 2005; Mancini, 2009), supports the hypothesis that this could have been an open grassland steppe, with shrub patches, similar to Pampean region for the same time span.

As regards the archaeological evidence (taxonomic and anatomic abundance) of guanaco, undoubtedly it is the most important species in the sites since the beginning of the human occupation in both regions. Nevertheless, in this group, the social appropriation goes beyond the economic sphere involve that social and imaginary domains, since the artistic representation of these animals appears in several places of Patagonia until late Holocene (Miotti and Carden, 2007 and reference therein).

The zooarchaeological contexts grouped by intervals (Table 3 and Fig. 6) indicate that those of the first interval (16 - 10 Ka BP) show a greater biodiversity than those of the second interval (9.9–8.7 Ka BP). For this span only horses and *Lama gracilis* persisted. Besides, during this span, the presence of *Lama guanicoe* is increased in number of individuals and of represented anatomic parts in all the considered sites.

In this case, the general trend of the first times became a hunting strategy of specification of resources, centered in the most popular species, the guanaco, with few cervid representatives in northern sites of the region, on the other hand, the only survivors of Pleistocenic Lujanian fauna in Patagonia.

The information gathered in this work, resulting from a myriad of sites of Pampa and Patagonia does not allow stating the generalization made by Martínez and Gutiérrez (2011) about the use of guanacos, since this theory is based on the archaeological evidence of a single site: "Remarkably, in one archaeological site (Paso Otero 5, see, mammal record previous of the extinction showed a large exploitation of extinct mammals and a reduced one of guanacos (*Lama guanicoe*). After the extinction, hunting was concentrated on guanacos and other relatively small mammals. This could be the representation of an opportunistic behaviour that resulted after the extermination of the spectacular fauna of huge mammals that inhabited South America before the entrance of humans. (Martínez and Gutiérrez, 2011, pp. 61).

By the evidence discussed at regional scale we understand that megafauna extinction did not interrupt the social and symbolic use that humans made of these giants in Holocene, and that their extinction did not lead to a more opportunistic use of smaller species, but rather, since the beginning of the human settling in both regions, the food subsistence basis was in guanacos, being the extinguished species of complementary and opportunist use.

As regards hairy xenarthrans, during the first interval it is scarce the representation of individuals and their anatomic parts in the archaeological sites, with which the most feasible hypothesis is that these animals formed part of the colonization landscape of the first humans in the region, but their use would be complementary or

opportunistic. If there was really a human intention of consumption, this was occasional. Only chopping patterns of these “allegedly preys” were detected in few sites such as Piedra Museo (Marchionni and Vázquez, 2012) and Arroyo Seco 2 (Politis et al., 2014; Gutiérrez and Johnson, 2014). Another use given to bones belonging to these animals was as fuel, as seen in Paso Otero 4 (Gutiérrez et al., 2010; Martínez and Gutiérrez, 2015). There are no artifacts made of these bones what means that this hypothesis of their use as part of technology is even weaker. However, in some cases, the mylodon association of a big deal of dermal little bones as in Cueva Fell, and El Trébol, and large bones used as fuel in Paso Otero 4, may be indicating that these first settlers of Patagonia might have used these animals' leather and bones for different social and symbolic practices.

The coexistence between the first explorers and Pleistocene megafauna could have been in stages according to different taxa and environmental differences in both regions. In Patagonia (12.5 Ka BP) it would begin 1000 years before and besides it would finish 1000 years before than in Pampa (ca. 7 ka BP). The large carnivores do not have archaeological record in Pampa, whereas in Patagonia, though with a low record, it is considered that they were used somehow by the first settlers (Table 6). The images of great felines are present in rock art and in the zooarchaeological record from the presence of paws and tusks. In Magallanes, *Arctotherium* sp, *Smilodon* sp, and a similar genus of xenarthra are also recorded (Mena and Reyes, 2001; Labarca, 2015), the latter with an archaeological record of a paw in the site Túnel of Santa Cruz central plateau (Skarbun et al., 2015).

Even though in Pampa region, the species *Panthera onca* (jaguar) had a distribution until the beginning of the 20th century, for this region and from the zooarchaeology, we conclude that the extinct subspecies *Panthera onca mesembrina* was coeval but was not used by the first settlers of this region (Table 6).

Teeth and paws of these felines are pieces of high preservation in the archaeological and paleontological records, as a result, if this species played a role in the cosmivision of the first settlers of both regions, it could be expected that they had been collected by the first settlers, even without ever having had the intention of hunting these carnivores. However, the zooarchaeological evidence of these elements is very fragmented, appearing in three sites so far (Caves Túnel de La María; El Ceibo and Cueva del Medio).

The only representation of a large feline in rock art of cave 6 of El Ceibo, although it is scarce evidence, supports the hypothesis of a social and symbolic appropriation of these animals, at least for the Patagonian area. However, it must be discarded the idea of economic use, or programmed hunting of these large felines. Both pieces of evidence account for a social knowledge and symbolic use of these animals (Rockman, 2003), which could have remained for many generations in the collective imaginary, even after their extinction. This collective memory may indicate that these animals certainly entered the cosmologic sphere of the first settlers, that is why, their appropriation expressed in images and in tooth and paw recollection would evoke their presence in the social collective of the first hunter-gatherers.

It is worth highlighting that in several societies, from current hunter-gatherers, such as Nukak groups from Amazonia, to Andean state societies (Dillehay and Kaulick, 1984–85; Saunders, 1998), the jaguar figure is conceived as one of a supernatural being with great power. This power could be transferred or granted to people through the possession of paws and tusks or the leather of these animals. Possessing these pieces, in general, did not result from the chasing and systematic hunting of these carnivores, but rather from collecting them after finding dead individuals. In this sense, it is worth thinking about the social importance that a tooth collar acquired, since for manufacturing it, dozens of elements were

necessary and long time was spent as it was not frequent to find dead jaguars every day. On the other hand, these collars could have been prestigious artifacts of hereditary type, what means that we can trace a biography (Gosden and Marshall, 1999). This allows inferring that their finding in a definite historic context is the result of a cultural tradition which could have started hundreds of years ago.

The gomphotherid group belonging to immigrant holarctic megafauna is scarcely represented in Pampa and Patagonia regions. It is only recorded in Monte Verde site, in the north of Patagonia, (Fig. 1). In the earliest occupational context, the abundance of *Cuveronius* sp. genus is of a NISP = 268 specimens, corresponding to a MNI of 1 individual (Dillehay, 1997). The cutmarks and usefulness are mostly represented in task fragments, what allows inferring a human opportunistic profit of any individual found dead, that is why, the hypothesis about programmed hunting of these proboscideans is discarded.

9. Conclusions

The extinction event was certainly spectacular. Some authors have referred to it as a mass extinction (Marshall et al., 1984; La Violette, 2011). However, it was not. Coexistence between first human explorers and Pleistocene megafauna and large mammals was differential in time in each species process. Nonetheless, coexistence remained ca. 5000 years since first humans arrived in Pampa and Patagonia. Human/fauna relationships started and finished ca. 1000 years before in Patagonia (Fig. 6).

In Pampa the occurrence of few species of Lujanian stock in archaeological contexts (ca. 7.5 Ka BP) allows us to infer that glyptodonts were economically exploited, and probably also socially and symbolically used for longer time than in Patagonia.

Scouting landscapes (12–11 Ka BP) in Patagonia, and (11–10.5 Ka BP) in Pampa had a lot mega mammals and large mammals available for new hunter-gatherer groups. The greatest biodiversity is recorded in Pampa, in Arroyo Seco 2 site (12 taxa), followed by sites in Patagonia, with the greatest records in Cueva Lago Sofía 4 (5 taxa) (Tables 1 and 2).

Colonization landscapes (11–8.5 Ka BP) in Patagonia, and (10.5–7. ka BP) in Pampa had different economic, social and symbolic incidence of the extinct fauna.

In Patagonia region the main resource hunted was *Lama guanicoe*, meanwhile *Hippidion* and *L. gracilis* were complementary, and Ground giant sloths were occasional. Only some parts of *Panthera onca* and other great carnivores were used, and these parts may have been obtained from finding dead animals but no from hunting.

However, interaction human/animals should have been a high impact on social and symbolic spheres (Table 6). Archaeological record in rock art and daily contexts reinforces this hypothesis.

In Pampa *L. guanicoe* was the main species exploited, *L. gracilis*, and ground sloths were occasional and/or complementary resources.

As regards camelids, even though *Lama gracilis* and *Hemiauchenia paradoxa* were available in both regions until ca. 9 Ka BP, the evidence of use of both is stronger in the Patagonian region than in that Pampean, where it can be inferred only the coexistence but not the human use.

Thus, those of greater chances of a taxa-human coexistence span were xenarthrans cingulates in Pampa and equids in Patagonia. Therefore, equids are outstanding in Patagonia as economic, social and symbolic resource, whereas the Pampean evidence is even weaker to be able to infer relevance in any of these three aspects in this region.

9.1. In short

What happened when megafauna became extinguished?

Palaeo-environmental aspect generated several consequences in restructuration of climates, biota, and water distribution, producing huge changes for landscapes in both regions. However, from the human point of view, we can say that the changes were economically smaller. In both regions the guanacos were the main faunal resources, however, other species like birds, armadillos, rodents and cervids were used as complementary, and promoted a generalist hunter strategy since the first human occupations.

However, from the social and symbolic appropriation the Pleistocenic giants probably were important beings which after their extinction became myths and legends, remaining among Pampean and Patagonian people long time.

In scientific thought we are in agreement *“If those giant Pleistocenic bugs encourage our curiosity, maybe, despite being extinct, they will continue somehow alive just like some hundreds of centuries ago”*. (Fariña and Vizcaíno, 1995, pp. 97).

Aknowledgments

We thank colleagues for help provided along the way, Alberto Cione for discussions concerning the Pleistocene mammals at issue in this paper, Darío Hermo, Rafael Suárez and the anonymous referees for valuable comments on the manuscript, and Diego Gobbo for creating the map. This work was done within the framework of the projects PICT-ANCYT-176 and PI-665 UNLP.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quaint.2018.01.004>.

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