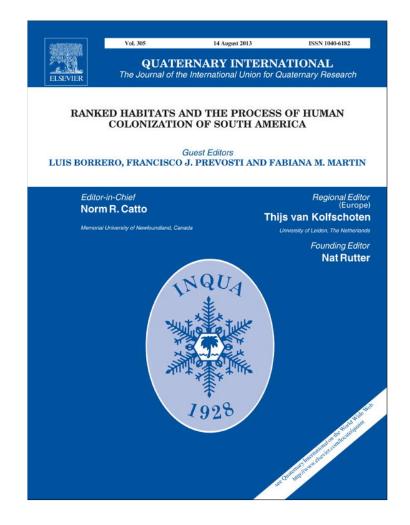
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Quaternary International 305 (2013) 127-140

Contents lists available at SciVerse ScienceDirect



Quaternary International

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

Holocene stability and recent dramatic changes in micromammalian communities of northwestern Patagonia

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ARTICLE INFO

Article history: Available online 7 August 2012

ABSTRACT

Micromammalian fossil sequences of two classical archaeological sites, Cueva Traful I (CTI) and Cueva Epullán Grande (LL), both in the province of Neuquén, northwestern Patagonia, Argentina, were studied. These sequences cover the entire Holocene, with assemblages mainly composed by rodent and marsupial remains accumulated by owls. Both sites are located near the ecotone fringes of the major vegetation units currently present in Patagonia: Forest-Patagonian steppe (CTI) and Patagonian steppe-Monte desert (LL). Comparisons between fossil and recent owl pellet samples in a regional approach indicated that micromammal communities remained stable over the major part of the last 10 ka, with some minor expansion of desert adapted taxa to the west since the middle Holocene, and a dramatic change in the assemblages during the last 100-150 years. Two alternative but not contradictory explanations can be presented to interpret the stable period. First, climate-environmental changes were not of sufficient magnitude to produce a clear reorganization of micromammal communities. Forest did not invade CTI surroundings, and Monte did not reach around LL. Second, the basic structure of northwestern Patagonian steppe micromammal communities was resilient to minor or moderate climate-environmental changes. The strong shift depicted in the studied sequences in very recent times (100–150 years) can be linked to human impact on the regional environment. This change involves a deep restructuration of small mammal communities ranging from virtual extirpations of some species to dramatic increments of opportunistic taxa. A century of sheep overgrazing, coupled with the introduction of exotic shrubs, was the main factor driving the configuration of present small mammal assemblages in northwestern Patagonia.

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1. Introduction

Despite the advances in the knowledge of Patagonian small mammals (e.g., Lessa et al., 2010; Patterson, 2010), stratigraphical sequences of micromammals remains have been scarcely addressed as a source to understand Quaternary climatic-environmental fluctuations in southern South America (e.g., Pardiñas et al., 2011 and references therein). This can be attributed more to the difficulties associated with reliable taxonomic identifications or interpretations of these remains as paleoenvironmental indicators than with the abundance or the intrinsic value of this proxy. More than four decades of detailed archaeological work in northwestern Patagonia retrieved several long Holocene sequences rich in small mammal bones (e.g., Mengoni Goñalons and Silveira, 1976; Silveira, 1979; Crivelli Montero et al., 1993, 1996; Hajduk et al., 2004).

* Corresponding author. E-mail address: ulyses@cenpat.edu.ar (U.F.J. Pardiñas). Regrettably, most of these assemblages remain unstudied or, in the best of the cases, unpublished (e.g., Pardiñas, 1999).

Cueva Traful I (CTI, thereafter) and Cueva Epullán Grande (LL) are classical archaeological sites in northwestern Patagonia (Borrero, 1999). The former, excavated in the late 1970s and early 1980s, is a cave with continuous Holocene sedimentation and complex stratigraphy (Crivelli Montero et al., 1993). The abundant micromammal remains obtained from this deposit were studied by Pearson and Pearson (1993; see also Pearson, 1987; Monjeau, 1989; Pardiñas, 1999). These authors concluded that no evident faunal changes were found along the sequence beyond the virtual disappearance, in very recent times, of the sigmodontine rodent Euneomys. Excavations in LL were conducted during the late 1980s and early 1990s (Crivelli Montero et al., 1996). Also with a complex stratigraphy, this cave yielded remains from ca. 10,000 years ago to the present. During this temporal segment, several nests and roosts were used by owls inside the cave, and their pellets incorporated in the sediments form a rich micromammal deposit (Pardiñas, 1999). Two preliminary contributions addressed the paleoenvironmental





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significance of these remains, recognizing the lack of major changes depicted by successive rodent assemblages (Crivelli Montero et al., 1996; Pardiñas, 1999).

This paper reanalyzes the micromammalian assemblages of CTI and LL using a regional approach based on comparisons over a broad range of recent owl pellet samples. Both sites are now located near the ecotone of the three major vegetation units that occur in Patagonia: Forest, Patagonian steppe, and Monte desert. This fortunate situation theoretically determinate their utility (and the aggregate value) to reflect potential changes suffered by the boundaries of these main vegetation formations during the Holocene.

2. Materials and methods

2.1. The caves

CTI (40° 43′ S; 71° 07′ W, 760 m, Los Lagos, Neuquén, Argentina; Fig. 1) is a multicomponent archaeological site near Confluencia. The cave is 20 \times 7 m and the inside surface is partly covered by large rock blocks. The stratigraphy of CTI encompasses 20 sedimentary layers, including several of wall-rock debris of few centimeters in thickness (Crivelli Montero et al., 1993). The site is open to the Traful river valley and is located in the Subandean District of the Patagonian Phytogeographical Province (sensu León et al., 1998). The general landscape around CTI shows a mosaic of shrubby steppes, naked rocky expositions, dwarf forest patches of *Nothofagus*, and isolated trees of *Austrocedrus chilensis* and *Maytenus boaria* (Crivelli Montero et al., 1993; Pearson and Pearson, 1993).

LL (40° 23′ 21″ S; 70° 11′ 40″ W, 680 m, Collón Curá, Neuquén, Argentina; Fig. 1) is also a multicomponent archaeological site about 40 km SW Piedra del Águila. This cave is about 7×5 m and is open to a small temporary creek. The stratigraphic sequence of LL is composed by sedimentary layers ("strata") and more restricted units ("structures") that were excavated using specific archaeological methodology for complex sites (Harris' matrix; see Crivelli Montero et al., 1996). LL is about 5 km north of the Limay river valley and the general landscape has shrubs of the genus *Larrea, Mulinum*, and *Schinus* developed on exposed sandy soils, large but

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Cueva Traful I sequence: Stratigraphy, chronology, and units selected for this study (main data after Crivelli Montero et al., 1993).

Stratigraphic unit	Date	Units in this study	Approximate chronology
Layer #1	No date	Pooled	Latest Holocene
Layer #2	No date	(Layer #1-2)	(XVIII-XX centuries) ^a
Layer #3	2230 ± 40	Pooled	Late Holocene
Layer #4	2720 ± 40	(Layer #3-4)	
Layer #5	No date (tefra)	Pooled	Late Holocene
Layer #6	No date	(Layer #5-6)	
Layer #7	No date	Pooled	Middle Holocene
Layer #8	No date	(Layer #7-9)	
Layer #9	$6030\pm115/$		
	6240 ± 60		
Layer #10	No date	Pooled	Early Holocene
Layer #11	No date	(Layer #10-15)	
Layer #12	No date		
Layer #13	$7308\pm285/$		
	7850 ± 70^{b}		
Layer #14	No date		
Layer #15	6870 ± 250^{c}		
Layer #16	No date	Pooled	Early Holocene
Layer #17	No date	(Layer #16-17)	
Layer #18	9430 ± 230	Pooled	Early Holocene
Layer #19	No date	(Layer #18-20)	
Layer #20	No date		
Layer #21	9285 ± 105^{c}	-	-

^a Both uppermost layers of CTI sequence include sheep feces.

^b An additional radiocarbon date for this layer gave the age of 9285 ± 313 (LP-62) but was discarded by excavators according to contamination reasons.

^c This radiocarbon date was discussed by excavators as contaminated.

low tablelands of pyroclastic rocks, and restricted filiform wetlands (regionally called "mallines") composed of green grasslands and patches of *Cortaderia selloana*. Phytogeographically, LL belongs to the Monte-Patagonia Ecotone (sensu León et al., 1998). This floristic unit penetrates the Occidental District of the Patagonian Phytogeographical Province following the course of the Limay River (Fig. 1). Additional information for both sites can be retrieved from several contributions that addressed a variety of archaeological aspects (e.g., Crivelli Montero and Fernández, 1996; Cordero, 2010, 2011).

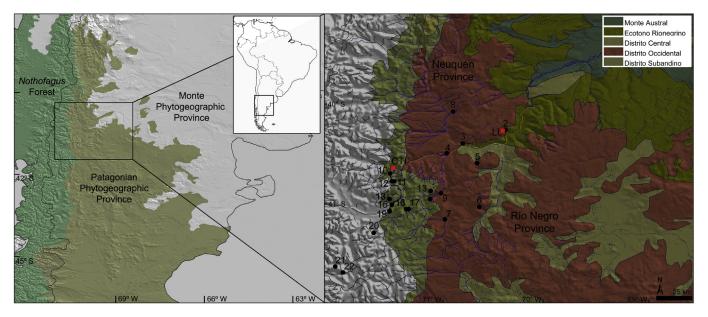


Fig. 1. Map of the study area, northwestern Patagonia, Argentina, with recording localities of fossil and recent studied samples superimposed to the main phytogeographic units (according to León et al., 1998). Numbers are those used in Table 4; CTI = Cueva Traful I, LL = Cueva Epullán Grande.

Cueva Epullán Grande sequence: Stratigraphy, chronology, and stratigraphical units selected for this study (main data after Crivelli Montero et al., 1996).

Stratigraphic unit	Date (radiocarbon years BP except noted)	Units in this study	Approximate chronology
Strata #1	No date	Pooled	Latest Holocene
Strata #2	1889–1904 AD ^a	(Strata #1–2)	(XVIII-XX centuries)
Tefra	2200 ±	-	-
	$60/2220\pm50^{\rm b}$		
Strata #3	$1720 \pm$	Strata #3	Late Holocene
	$50/2190 \pm 60$		
Structure #19	No date	Structure #19	Late Holocene
Strata #4	No date	Strata #4	Middle to Late
			Holocene
Strata #5	5140 ± 70	Strata #5	Middle Holocene
Strata #6	7060 ± 90	Strata #6	Middle Holocene
(lower part)			
Strata #7	$7900 \pm$	Pooled	Early Holocene
(upper part)	$70/7550 \pm 70$	(Strata #7)	
Strata #7	9970 ± 100		
(lower part)			

^a Dates from newspaper fragments found inside this strata.

^b These radiocarbon dates are from the stratigraphical sequence of the Cueva Epullán Chica, a smaller cave about 100 m away from LL.

2.2. Fossil samples and chronology

Micromammalian assemblages from CTI were mainly addressed based on the data provided by Pearson and Pearson (1993) and complemented with additional samples (MNI = 519) of this site (layers #1-2 [MNI = 12], layers #5-6 [217], layers #7-9 [165], layers #10-15 [132]) studied by one of the authors (PT); those from LL were reanalyzed from Pardiñas (1999). Stratigraphic units and chronological data are provided in Tables 1 (for CTI) and 2 (for LL). Minimum number of individuals (MNI) per stratigraphic unit is provided in Table 3. Chan et al. (2005) and Chan and Hadly (2011) reported additional ages for CTI based on direct dating of micromammal bones. Some minor differences between these chronologies and those previously reported by the archaeologists that excavated the cave (see Crivelli Montero et al., 1993) were detected, especially towards the upper level of the sequence. However, Chan et al. (2005) and Chan and Hadly (2011) did not discuss these incongruences, or their combination of levels into temporal intervals, and even the number of intervals considered (four in Chan et al., 2005 and three in Chan and Hadly, 2011) was not adequately explained. For these reasons, the chronological and stratigraphical framework published by Crivelli Montero et al. (1993) is used, combining archaeological, faunal, and stratigraphical evidence.

2.3. Taphonomy

The micromammal assemblages from both sites were mainly produced by the trophic activities of owls (Pearson and Pearson, 1993; Pardiñas, 1999, 2000). In CTI, osseous remains of small mammals composed discrete accumulations in the form of circumscribed deposits or pockets, and some hydrological minor reworking was inferred (Crivelli Montero et al., 1993). Dryness in LL allowed the preservation of intact owl pellets in several layers, especially from the middle and upper levels. An almost "fresh" sample of 89 pellets plus disaggregate osteological material was found in structure #19, all indurated with owl feces, vertically in an ancient wall roost. Taking into account the low degree of bone and teeth corrosion observed in the samples from LL and CTI, it is probable that the Common Barn Owl, *Tyto alba*, was the main participant in the formation of these assemblages (cf. Pardiñas, 2000). Other taphonomic agents aside from owls cannot be discarded as accumulators of micromammal remains in both studied sequences. At least for LL, several traits on bone remains (e.g., burns, breakage pattern; Medina et al., 2012) suggest that human practices added large rodents including the caviomorph *Ctenomys* spp., and the cavies *Galea leucoblephara* and *Microcavia australis* to the record (Pardiñas, 1999; see discussion below).

2.4. Modern samples

Comparisons focused on exploring the paleoenvironmental significance of archaeological samples were performed using a wide range of recent owl pellet samples of Bubo magellanicus and T. alba recovered from nest and roosting sites across the study area (Table 4). These samples reflect the main phytogeographical units that occur in northwestern Patagonia (Forest, Subandean District, Occidental District, Central District, and Monte-Patagonia Ecotone, sensu León et al., 1998). A representative sample (locality #1, Table 4) from the Monte Phytogeographical Province (Fig. 1) was also analyzed. Original comparisons for CTI made by Pearson and Pearson (1982, 1993) used trapping data from the surroundings of the site. This approach is inaccurate due to several differential biases involved in the faunal representation provided by owls and traps (see Torre et al., 2004). To solve this problem, a T. alba pellet sample collected in the interior of CTI during 2010 was included. In addition, several other assemblages produced by B. magellanicus (Massoia et al., 1991) and T. alba (Trejo and Lambertucci, 2007) recovered less than 10 km south of CTI (localities #10-12, Table 4) were used. For LL, there are 3 years of pellet samples collection (1989–1991; breeding and non-breeding seasons) of T. alba in the vicinity of the site (<200 m; locality #2, Table 4) that forms a suitable recent sample to compare with archaeological ones. Comparisons beyond northwestern Patagonia, restricted to explore some particular topics (e.g., Euneomys spp. abundance pattern), were performed using a large unpublished database composed of more than 250 modern owl pellet samples (with MNI > 100) covering all Patagonia.

2.5. Patagonian micromammal assemblages as environmental indicators

Several previous contributions addressed the value of Patagonian micromammal assemblages derived from owl pellet analyses as environmental indicators (e.g., Pearson and Pearson, 1993; Pardiñas, 1998, 1999; Andrade and Teta, 2003; Teta et al., 2005; Pardiñas and Teta, 2008; Fernández et al., 2011, 2012; Pardiñas et al., 2012). The analysis of 58 owl pellet samples of B. magellanicus and T. alba covering northern Patagonia from the Atlantic coast to the Andean piedmont showed that small mammal assemblages are useful to characterize both main and minor phytogeographical units (Pardiñas et al., 2003). Similar results were replicated by Trejo and Lambertucci (2007) using a smaller set of samples of T. alba pellets from roughly the same area. Regarding ecological requirements of marsupials and rodents occurring in northwestern Patagonia, successive contributions made by Pearson (1983, 1984, 1987, 1995; see also Monjeau, 1989) provide the basic data for the interpretations developed here. Small mammal distributions along a W-E transect crossing the main phytogeographical units that occur in northwestern Patagonia are summarized in the Fig. 2.

2.6. Paleoenvironmental reconstruction

The rationale behind paleoenvironmental reconstruction methodology employed in this paper is based on two partially

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Table 3

Minimum number of individuals in the stratigraphic units of Cueva Traful I (CTI) and Cueva Epullán Grande (LL); taxa are arranged in alphabetical order.

	Abrothrix longipilis	Abrothrix olivaceus	Akodon iniscatus	Akodon neocenus	Chelemys macronyx	Ctenomys spp.	Eligmodontia sp.	Euneomys spp.
CTI, layer #1-2	17	0	0	0	27	51	1	110
CTI, layer #3-4	63	10	0	0	97	166	1	281
CTI, layer #5-6	12	0	0	0	16	59	0	51
CTI, layer #7-9	33	3	0	0	123	261	6	442
CTI, layer #10-15	13	1	0	0	25	49	0	113
CTI, layer #16-17	28	3	0	0	19	62	0	149
CTI, layer #18–20	12	3	0	0	18	32	0	69
LL, strata #1—2	0	0	1	4	1	52	19	1
LL, strata #3	1	0	1	0	0	135	8	5
LL, structure #19	2	4	1	1	2	89	27	8
LL, strata #4	2	1	0	0	3	47	14	7
LL, strata #5	1	1	0	0	0	94	8	4
LL, strata #6	0	0	1	0	0	98	17	6
LL, strata #7	2	9	3	0	0	313	66	27

Table 4

Minimum number of individuals in modern owl pellet samples from northwestern Patagonia (Neuquén and Río Negro provinces) used in this study. Numbers in the first row are those used in Fig. 1; taxa are arranged in alphabetical order.

	Locality	Abrothrix longipilis	Abrothrix olivaceus	Akodon iniscatus	Akodon neocenus	Calomys musculinus	Chelemys macronyx	Ctenomys spp.	Dromiciops gliroides	Eligmodontia spp.	Euneomys chinchilloides	Galea leucoblephara	Geoxus valdivianus
1	San Carlos	0	0	0	3	0	0	9	0	84	0	2	0
2	Cañadón del Tordillo	1	93	37	1	1	0	4	0	218	2	0	0
3	Confluencia	2	1	0	17	93	0	13	0	36	0	0	0
4	Cerro Castillo	1	6	0	7	0	0	38	0	104	0	1	0
5	Cañadón A° Fuquelen	0	15	0	0	0	0	29	0	28	0	0	0
6	10 km WNW Comallo	4	18	0	0	0	0	8	0	159	1	0	0
7	Estancia Pilcañeu	11	74	0	0	0	0	44	0	61	18	0	0
8	Cerrito Piñón	0	1	2	0	1	0	48	0	15	0	3	0
9	Paso de Los Molles	1	36	4	0	0	0	15	0	10	0	0	0
10	Valle Encantado	56	5	0	0	0	7	17	0	23	0	0	5
11	La Lipela	119	11	0	0	0	0	13	0	14	3	0	0
12	La Lipela	2	4	4	0	0	0	2	0	3	1	0	4
13	Pipilcura	19	15	0	0	0	7	27	0	1	4	0	1
14	Cooperativa Escuela	19	51	0	0	0	3	14	0	25	12	0	0
15	Río Limay	9	9	0	0	0	3	14	0	1	5	0	2
16	San Ramón	36	15	0	0	0	3	15	0	21	0	0	2
17	Laguna Los	25	12	0	0	0	1	10	0	8	0	0	0
18	Juncos Ea. Fortín Chasabusa	11	5	0	0	0	0	0	0	0	0	0	0
19	Chacabuco Cerro Leones	566	393	0	0	0	27	50	0	169	23	0	18
20	Chalhuaco	59	1	0	0	0	44	20	3	6	3	0	18
21	Lago Steffen	7	36	0	0	0	1	0	0	0	0	0	2
22	Cabaña Cacique Foyel	6	11	0	0	0	0	0	0	0	0	0	1
23	Cueva Traful (recent)	7	3	0	0	0	7	0	0	2	0	0	3

^a Oliver Pearson unpublished field notes housed at Museum of Vertebrate Zoology Library (Berkeley, California).

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Galea leucobephara	Geoxus valdivianus	lrenomys tarsalis	Lestodelphys halli	Loxodontomys micropus	Microcavia australis	Notiomys edwardsii	Octodon bridgesii	Oligoryzomys longicaudatus	Phyllotis xanthopygus	Reithrodon auritus	Thylamys pallidior	Total
1	2	2	1	71	0	0	2	2	13	17	0	317
2	2	1	3	213	0	0	2	2	89	86	0	1018
0	0	1	0	64	1	0	4	1	4	4	0	217
1	2	6	0	255	0	0	9	2	38	49	0	1230
0	1	2	0	71	0	0	3	3	4	8	0	293
0	3	1	0	152	0	0	2	2	9	6	0	436
0	0	0	0	40	0	0	1	0	5	2	0	182
0	0	0	1	3	5	0	0	4	13	33	4	141
1	0	0	0	2	9	0	0	0	24	35	1	222
2	0	0	0	2	9	0	0	0	102	90	0	339
0	0	0	0	1	4	0	0	0	39	34	0	152
0	0	0	0	1	2	0	0	0	17	18	1	147
1	0	0	0	0	4	0	0	0	46	30	2	205
1	0	0	0	6	27	1	0	7	173	80	5	720

Graomys griseoflavus	Irenomys tarsalis	Lestodelphys halli	Loxodontomys micropus	Microcavia australis	Octodon bridgesii	Oligoryzomys longicaudatus	Phyllotis xanthopygus	Reithrodon auritus	Thylamys pallidior	Total	LS	LW	Main reference
23	0	0	0	9	0	0	0	3	3	136	40°02′	67°56′	This paper
0	0	0	0	0	0	11	78	58	8	512	40°23′	70°11′	Pardiñas et al. (2003)
0	0	0	0	1	0	23	3	18	0	207	40°30′	70°32′	Massoia (1988)
0	0	5	2	0	0	5	29	58	0	256	40°35′	70°40′	Pardiñas and Massoia (1989)
0	0	8	0	0	0	2	7	26	2	117	40°40′	70°25′	Pardiñas et al. (2003)
0	0	3	3	4	0	2	18	16	3	239	41°02′	70°24′	O. Pearson unpublished ^a
0	0	11	5	0	0	0	4	111	0	339	41°08′	70°41′	Pardiñas et al. (2003)
0	0	0	0	7	0	1	2	38	0	118	$40^{\circ}14'$	70°37′	This paper
0	0	2	0	0	0	0	1	20	0	89	40°55′	70°43′	Pardiñas et al. (2003)
0	19	0	69	0	0	74	11	2	0	288	40°45′	71°08′	Trejo and Lambertucci (2007)
0	6	0	96	0	0	64	2	31	0	359	40°49′	71°06′	Trejo and Lambertucci (2007)
0	4	0	7	0	1	9	13	1	0	55	40°49′	71°07′	Massoia et al. (1991)
0	0	0	27	0	0	1	2	31	0	135	40°54′	70°48′	Trejo and Lambertucci (2007)
0	0	0	19	0	0	0	8	18	0	169	40°58′	70°48′	Trejo and Lambertucci (2007)
0	1	0	18	0	0	13	11	28	0	114	41°01′	71°07′	Massoia and Lartigau (1995)
0	2	0	22	0	0	36	16	72	0	240	41°03′	70° 59′	Trejo and Lambertucci (2007)
0	0	0	51	0	0	6	1	54	0	168	41°03′	$71^{\circ}00^{\prime}$	O. Pearson unpublished ^a
0	0	0	49	0	0	18	27	8	0	118	40°58′	71°08′	O. Pearson unpublished ^a
0	20	0	621	0	0	508	19	361	0	2775	41°04′	71°08′	O. Pearson unpublished ^a
0	0	0	84	0	0	42	2	6	0	288	41°15′	71°16′	Trejo and Lambertucci (2007)
0	7	0	19	0	0	29	0	0	0	101	41°32′	71°35′	Udrizar Sauthie et al. (2005)
0	6	0	21	0	0	38	0	0	0	83	41°35′	71°31′	Udrizar Sauthie et al. (2005)
0	0	0	7	0	0	85	2	0	0	116	40°43′	71°07′	This paper

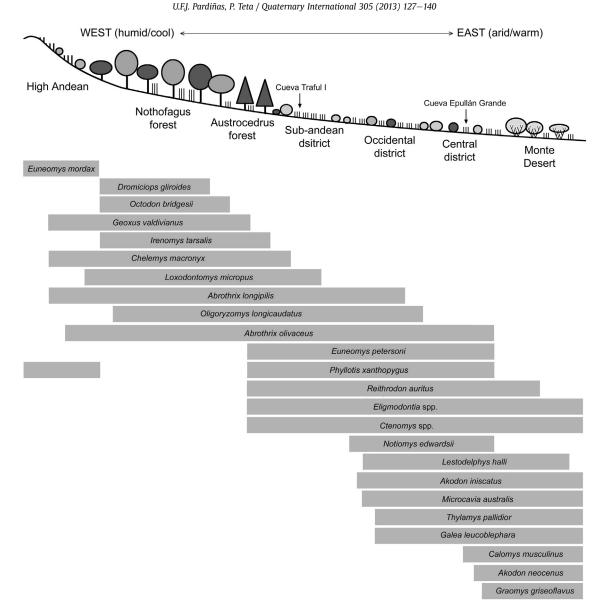


Fig. 2. Distribution of rodent and marsupial species along west-east gradient in northern Patagonia (compiled from several sources).

untested assumptions: (1) trophic behavior of past owls involved in the assemblages formation does not significant depart from those observed in modern owls (e.g., forage radio around nest in T. alba remains in <5 km through Holocene); (2) archaeological micromammal assemblages "capture" the main structural pattern of past communities rather than minor deviations due to catastrophic events (e.g., mass outbreaks). Assumption (1) is coherent with the short time elapsed from the fossil record formation. Assumption (2) is coherent with the nature of the fossil record, in moderately continuous sedimentary sequences with moderate time averaging that produce a general dilution of particular events to retain the basic signature of biocenosis (see Pardiñas, 1999; Terry, 2008). Archaeological and modern samples were studied using cluster and ordination analyses after exploration of sample-size effects on their taxonomical structures. Cluster analyses were based on presence/ absence data matrix, with the Jaccard similarity coefficient calculated and UPGMA used to produce graphic outputs (phenograms; Digby and Kempton, 1987). Correspondence analyses were used to explore species and sample ordination in multivariate space (Greenacre, 1984) and were performed on a standardized octavescale method (Gauch, 1982) data matrix of relative abundances (% MNI).

3. Results and discussion

3.1. Taxonomic structure

Both studied sequences show approximate constancy of dominant taxa from lower to upper levels. CTI is characterized by high frequencies (>15% of total MNI) of *Ctenomys* spp., *Euneomys* spp., and *Loxodontomys micropus*. *Chelemys macronyx* is represented by lower values (3–10%) and *Abrothrix longipilis*, *Phyllotis xanthopygus*, and *Reithrodon auritus* ranged, with few exceptions, between 1 and 6% (Fig. 3). In the case of LL, high frequencies of *Ctenomys* spp. characterized all strata, followed by *P. xanthopygus* and *R. auritus* (9–30%) and *Eligmodontia* spp. (<14%; Fig. 3).

At least two species of *Ctenomys* are represented in each site. *Ctenomys* systematics are poorly resolved in Patagonia, where several morphologically very similar species occur (e.g., Pearson and Christie, 1985). Pearson and Pearson (1993; see also Chan

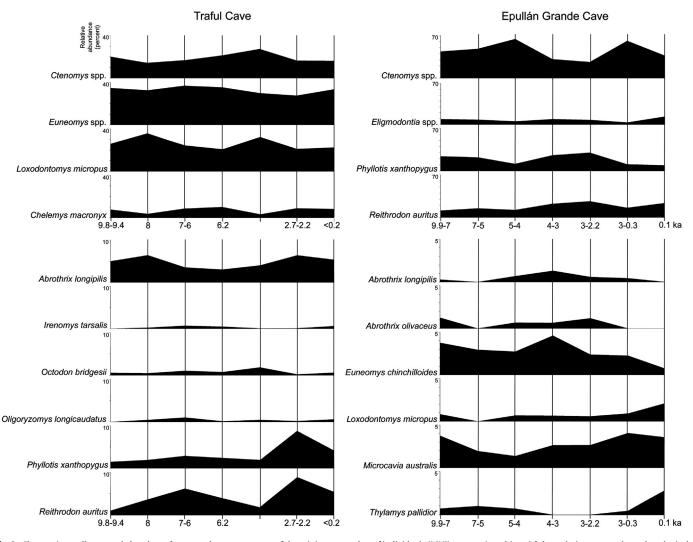


Fig. 3. Changes in small mammal abundance [expressed as a percentage of the minimum number of individuals (MNI) per stratigraphic unit] through time across the archaeological sequences of Cueva Traful I and Cueva Epullán; ka, radiocarbon kiloyears before present.

et al., 2005) highlighted the presence of two Ctenomys morphotypes in CTI sequence, a larger form, identified as Ctenomys sociabilis, and a smaller one and largely dominant, referred as Ctenomys haigi. The same situation was reported by Pardiñas (1999) for LL, where the larger form was ascribed to Ctenomys maulinus. As discussed by Pardiñas (1999, 2000), high frequencies of Ctenomys sp. characterize several archaeological sites in Patagonia. In some cases, the dominance of this rodent amounts to 90% (e.g., Cuyín Manzano; Ceballos, 1982). Almost all LL strata showed Ctenomys frequencies >30%, reaching 64% in strata #5. In clear contrast, Ctenomys representation in recent owl pellet samples is in general <10% (cf. Table 4). Pardiñas (1999, 2000) suggested taphonomical aspects and methodological biases related to the excavation techniques in order to explain the higher archaeological proportions of Ctenomys and other caviomorph rodents in the caves (e.g., the cavies G. leucoblephara and M. australis). Ctenomys and other large caviomorph rodents have strong skulls and mandibles and remain almost intact in depositional contexts, while those of several fragile and smaller sigmodontine rodents do not (Pardiñas, 1999, 2000). In caves where circulation space is restricted, fragmentation by trampling (by humans and animals) cannot be discarded and may favor the over representation of large rodents (i.e., Ctenomys and cavies). LL structure #19, with a micromammal assemblage derived from well preserved "fresh" owl pellets, shows the lowest *Ctenomys* proportion of all LL sequence. In addition, caviomorph rodents can be over-represented due to human past practices related to capture and consumption. At least for LL, evidence (differential burning and peculiar breakage pattern; see Pardiñas, 2000) indicates that a fraction of *Ctenomys, G. leucoblephara* and *M. australis* individuals were incorporated into the archaeological deposits by human activities. The human exploitation of these faunal resources was also reported from several Late Holocene contexts close to the caves, especially in Pilcaniyeu (e.g., Casa de Piedra de Ortega site; Pardiñas, 2000; Teta et al., 2005) and the valley of the Chubut river (e.g., Campo Cerda site; Pardiñas, 1999, 2000; Udrizar Sauthier, 2009).

An important point regarding paleoenvironmental issues is the possibility that past populations of *Ctenomys* were much more abundant than those in modern times. This issue was in general overlooked by previous studies (e.g., Pardiñas, 1999, 2000). Almost all travelers that crossed Patagonia during the 19th and the early 20th century reported conspicuous *Ctenomys* burrows, in many cases covering kilometers in extent (e.g., Hatcher, 1903). Today, *Ctenomys* burrows are rarely observed in the field and are mostly limited to small and well drained areas. *Ctenomys* has disappeared from a vast area of the Patagonian regions. Eradication or reduction

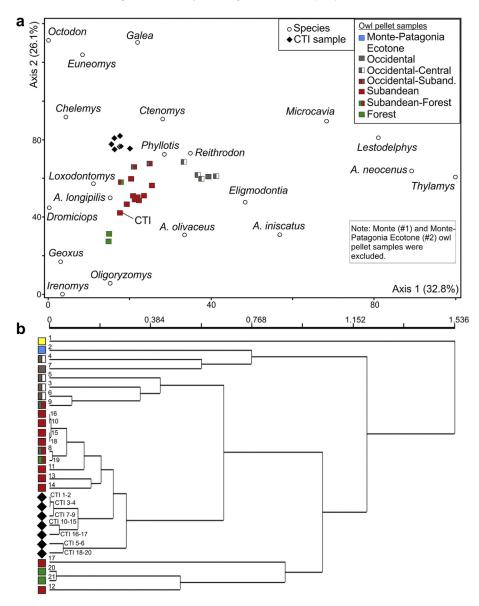


Fig. 4. Multivariate analyses of fossil small mammal samples of Cueva Traful I and recent owl pellet samples from northern Patagonia, (a) correspondence analysis, CTI indicates the location of the recent owl pellet sample collected inside the cave; (b) cluster analysis, numbers above branches are those used in Tables 3 and 4.

of *Ctenomys* populations in Patagonia was clearly a desirable consequence of sheep introduction, an issue raised by few authors (e.g., Osgood, 1943). Other subterranean rodents, such as the red vizcacha rat *Tympanoctomys*, were regionally extirpated by the same cause in the central Chubut river valley (Udrizar Sauthier et al., 2009; Pardiñas et al., 2012). *C. sociabilis* disappeared from the area of CTI before 3 ka, perhaps due to a combination of habitat reduction, competition with *C. haigi*, and the impact of volcanic eruptions (Chan et al., 2005; Chan and Hadly, 2011).

The representation of the medium-sized sigmodontine rat *Euneomys* spp. in CTI sequence is also conspicuous (20–40%), contrasting with its virtual absence in recent regional samples (cf. Table 4). This point was previously discussed by Pearson and Pearson (1993; also see Pearson, 1987) and more recently by Pardiñas (1999) and Rebane (2002). First, is necessary to note that two congeneric entities are present in CTI, a larger form identified as *Euneomys mordax* and a slightly smaller and widespread *Euneomys chinchilloides* (Pearson and Pearson, 1993). Morphological similarities and fragmentary remains make clear separation of both

species along CTI sequence almost impossible (see Pearson and Pearson, 1993). Solely for the assemblage of layer 3, Pearson and Christie (1991) attempted to quantify *E. chinchilloides* and *E. mordax* proportions, and obtained a representation of 95.2% (MNI = 179) and 4.8% (MNI = 9), respectively. The genus *Euneomys* is also represented in the sequence of LL, but by a single morphotype referable to *E. chinchilloides* and with frequencies <5%. No reliable taphonomic biases can be argued in order to explain the high proportions of *Euneomys* spp. in CTI beyond its past abundance in the field and owl diets.

3.2. Micromammal assemblages as past environmental indicators

Correspondence analysis made on standardized %MNI data matrix is consistent to classify CTI fossil assemblages close to those of Subandean and Occidental vegetational districts. However, CTI fossil samples are isolated with respect to the remainder, including the recent sample collected inside the cave. This isolation remains when some dominant taxa, such as *Euneomys* spp., are excluded from the analysis (Fig. 4a). Similar results were obtained from cluster analysis of presence/absence data matrix (Fig. 4b). This difference between recent and fossil samples can be also extracted from a direct inspection of the taxonomic structures involved (Tables 3 and 4). Modern samples #10–12 collected in CTI and within 10 km around CTI are characterized by the dominance of *A. longipilis, L. micropus*, and *Oligoryzomys longicaudatus*, followed by smaller frequencies of *Ctenomys* sp., *Eligmodontia* spp., and *Irenomys tarsalis*. In contrast, the CTI micromammal sequence shows the dominance of *Ctenomys* spp., *Euneomys* spp., and *L. micropus* throughout, with *A. longipilis* (<7%) and *O. longicaudatus* (<1%) scarcely represented.

The frequency of *Euneomys* spp. in several stratigraphical units of CTI reaches >30% (Fig. 3). Fig. 5a depicts Patagonian localities with recent occurrences of this rat in excess of 10%. Frequencies >30% characterize Patagonian steppe and Forest-steppe ecotones in western Santa Cruz and Chubut provinces, and the more restricted high altitude basaltic plateaus and associated hilly systems of Central Patagonia. All these areas are characterized by scattered grassland or shrub steppe vegetation under windy and cold conditions. On the other hand, L. micropus reaches >20% in several CTI stratigraphical units (Fig. 3). Fig. 5b shows Patagonian localities >10% for this rodent highlighting Forest and Foreststeppe ecotone areas in northwestern Chubut, Río Negro, and Neuquén provinces. Habitats of where these high proportions of Loxodontomys occur are characterized by dense dwarf Nothofagus patches or shrubby formations ("matorral") associated with dense grassland coverage and deep soils under mesic conditions. Modern co-occurrence of high proportions of both Euneomys and Loxodontomys in a single locality is almost non-existent. Ratios between Euneomys and Loxodontomys abundances in CTI are 1.5-1.8 in several stratigraphic units. Roughly comparable values were observed in a few owl pellet recent samples from more than 250 examined covering all of Patagonia. One of them is from Lago Burmeister, Cerro Casa de Piedra in Perito Moreno National Park area, western Santa Cruz province; two others are fresh pellets collected in western Chubut Subandean environments. All of these samples represent hostile hilly and windy treeless landscapes dominated by bunchgrasses in exposed soils with isolated patches of dense shrubby coverage.

Fossil assemblages from LL are plotted close to modern samples from Occidental and Central Districts, and Monte-Patagonia Ecotone. However, with the exception of Ctenomys sp., LL samples seem to occupy their own bivariate space (Fig. 6a). Cluster analysis indicates associations with Monte Desert and Occidental-Central modern samples. However, there is no close association with the recent sample (locality #2; Table 4; Fig. 6b). LL fossil samples depart consistently from the modern local assemblage, including high proportions of Ctenomys spp., P. xanthopygus, and R. auritus, low frequencies of *Eligmodontia* spp. (<10%) and negligible abundances of Abrothrix olivaceus. The recent assemblage is dominated by >40% Eligmodontia spp. plus significant frequencies of A. olivaceus and Akodon iniscatus. Recent high proportions of the silky mice Eligmodontia spp. mark northwestern Patagonian steppe samples (Pearson et al., 1987), usually associated with larger proportions of A. olivaceus and R. auritus (see Table 4). High proportions of Eligmodontia spp. characterize the Monte Phytogeographical Province (Table 4; see also Pardiñas et al., 2003 and Trejo and Lambertucci, 2007), always associated with considerable amounts of Graomys griseoflavus and the absence of A. olivaceus. As in the case of CTI, the sequence of LL is characterized by constant, although small, occurrences of Euneomys with a decreasing tendency in recent times.

3.3. CTI and LL paleoenvironments evolution according to small mammals

The small mammal assemblage of the oldest stratigraphic unit of CTI (layer #18–20, Early Holocene around 10—9 ka) lacks three typical forest and forest-steppe ecotone rodents, *Geoxus valdivianus, I. tarsalis*, and *O. longicaudatus*. The absence of these species plus the low values of *Octodon bridgesii* and the high values of *A. olivaceus* suggest a local landscape composed by more open environments than today and reduced forest patches under colder and probably drier conditions (see also Pardiñas and Teta, 2008). CTI layer #16–17 shows the first occurrence in the sequence of *G. valdivianus*, *I. tarsalis*, and *O. longicaudatus* and a higher

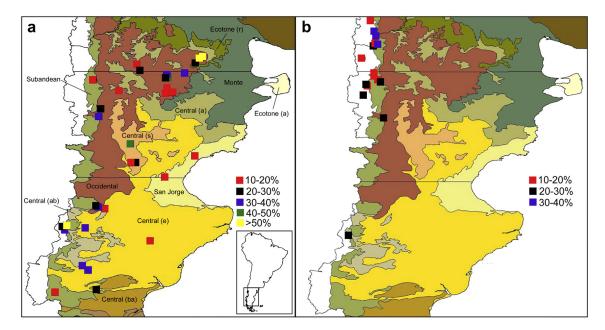


Fig. 5. Relative abundances [expressed as a percentage of the total minimum number of individuals (MNI) per sample] of *Euneomys* (a) and *Loxodontomys* (b) across Patagonia according to recent owl pellet samples.

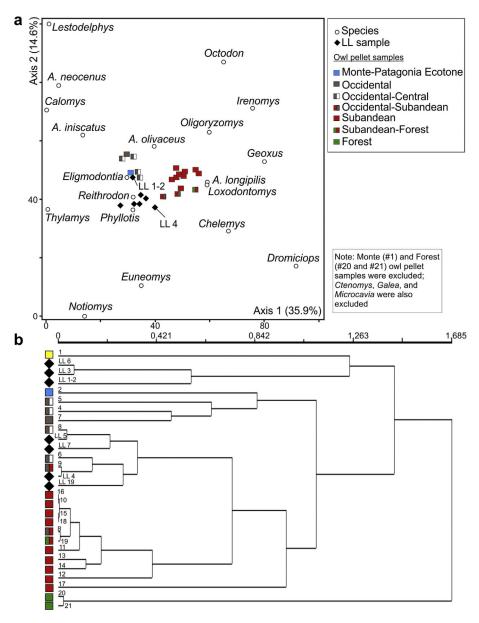


Fig. 6. Multivariate analyses of fossil small mammal samples of Cueva Epullán Grande and recent owl pellet samples from northern Patagonia, (a) correspondence analysis, light blue square indicates the location of the recent owl pellet sample collected around LL; (b) cluster analysis, numbers above branches are those used in Tables 3 and 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportion of *L. micropus* (>30%), indicating forest and shrubland expansion. By the end of Early Holocene and the beginning of Middle Holocene (layers #10–15 and #7–9), a smooth shift in micromammal communities around CTI can be inferred from the first occurrence of *Eligmodontia* spp. and the cavy *G. leucoblephara*. Both rodents are today typical of Patagonian arid environments, and their ingression to CTI surroundings is indicative of dryness. Coincidentally, these layers have the lowest values for *A. longipilis* and *L. micropus* in the sequence. During the Late Holocene, after a volcanic episode (marked by the layer #5–6 tephra; see Villarosa et al., 2006), two medium-size rats, *P. xanthopygus* and *R. auritus*, reach >8%. This, coupled with the first occurrence of a typical Occidental-Central Patagonian marsupial, *Lestodelphys halli*, appears to be indicative of open herbaceous steppes and rocky outcrops.

Despite the proximity of CTI to the recent forest boundary, the micromammal assemblages of this site reflect that neither dense forest nor Occidental vegetation environments, reached its surroundings during the entire Holocene. Typical forest assemblages are characterized by the presence of Dromiciops gliroides and G. valdivianus, moderate proportions of I. tarsalis, A. longipilis, and olivaceus, and high frequencies of L. micropus А. and O. longicaudatus (Pearson and Pearson, 1982). This taxonomic structure is not present in any single stratigraphic unit of CTI. Although the CTI sequence shows high frequencies of L. micropus, the sigmodontine rodents G. valdivianus, I. tarsalis, and O. longicaudatus never accounted for more than 1% in the last 10 ka. Several species usually associated with open arid environments are consistently absent or have minor proportions along CTI sequence. The evolution of *Eligmodontia* spp. in CTI, a taxon that characterizes Monte, Occidental, and Central assemblages, is conclusive to the general absence of a high proportion of semi-arid shrubland patches around the site. The same is indicated with respect to rocky exposures or grassland patches by the negligible values reached by *A. olivaceus* or the moderate and in general less than 5% for *P. xanthopygus* and *R. auritus*.

As CTI, the Early Holocene small mammal assemblage in LL (strata #7) also suggests more hostile and colder western environments than the present ones. These conditions can be interpreted from the single occurrence of a typical Occidental-Central sigmodontine rodent (Pardiñas et al., 2008), Notiomys edwardsii, coupled with moderate abundances of E. chinchilloides and L. micropus and the occurrence of O. longicaudatus. Moister but colder conditions during Middle Holocene (strata #5 and #4) seem to be evident by the presence of C. macronyx, a mole rat locally absent today. Late Holocene small mammal communities were enriched with the addition of Akodon neocenus, a typical Monte and Monte-Patagonia ecotone rodent. Structure #19, due its taphonomic nature, is a good window to infer Late Holocene environments around LL. From the taxonomic structure, it seems clear that the general landscape was composed of grasslands (high proportions of R. auritus) and rocky outcrops (high proportions of P. xanthopygus) with minor shrubland components (low proportions of A. iniscatus, A. olivaceus, and Eligmodontia spp., absence of the marsupial Thylamys pallidior). Furthermore, despite the proximity of LL to the recent Monte Desert boundary, this vegetation unit never reached the cave surroundings during the entire Holocene. The same can be asserted with respect to the Subandean District. In general terms, the micromammal sequence from LL suggests a smooth trend from more patent Patagonian Occidental-Central conditions during Early-Middle Holocene to Monte-Patagonia ecotone conditions for Late Holocene times.

Two main conclusions can be drawn from both micromammal sequences and their comparison with modern owl pellet samples. First, during the entire Holocene and despite minor variations (e.g., in the frequency of C. sociabilis in CTI) or trends (e.g., the progressive ingression of Monte elements along the Middle and Late Holocene of LL), small mammal communities around both sites remained basically stable. Micromammal assemblage stability is not necessarily a synonym of no environmental shifts. Two alternative but not exclusive hypotheses can be advanced in order to explain the results. On one hand, Holocene climate fluctuations in northwestern Patagonia were not strong enough to produce environmental changes capable of producing a deep alteration in the basic taxonomic structures of micromammal communities. On the other hand, the basic structure of northwestern Patagonian steppe micromammal communities was mostly resilient to minor or moderate climate-environmental changes. Perhaps, the micromammalian record as a paleoenvironmental indicator is, at least for this area, insufficient to reflect minor or moderate climateenvironmental changes and consequent minor vegetation shifts. However, contrary to this assertion, studies carried out involving modern owl pellet samples indicate that small mammal assemblages have an accurate fidelity to major and minor vegetation units (e.g., Pardiñas et al., 2003; Trejo and Lambertucci, 2007).

3.4. Micromammals and paleoclimate evolution of Northwestern Patagonia during Holocene

CTI and LL small mammal successions cannot be seen in isolation from the regional faunal dynamics during Holocene times in northwestern Patagonia (Pardiñas et al., 2011). Although this main topic is still poorly resolved, some indicators can be drawn from these archaeological sequences. At the end of the late-glacial period and the Early Holocene, open *Nothofagus* forests, supporting substantial amounts of steppe and shrubland elements, were widespread in the Eastern foothills of the Andes (e.g., Markgraf, 1984; Whitlock et al., 2006). The paleoclimatic model simulations for early-Holocene feature warm, relative dry winters and cool summers (Whitlock et al., 2001). In addition, awakened westerly flow apparently reduced effective moisture in the mid- and highlatitudes. In accordance, micromammal samples from CTI are characterized by lower specific diversity and by the absence of primary-*Nothofagus* forest sigmodontines (e.g., *Irenomys, Geoxus*), while the LL assemblages suggest lower moisture than present and a local landscape dominated by open rocky areas with sparse shrubby vegetation.

Around CTI, the *Nothofagus dombeyi*-type spores are best represented before 7.8 ka, and between 2.7 and 2.2 ka, suggesting more humid conditions and tree cover around these periods (Heusser, 1993). In agreement, there is a high representation of forest dwellers (e.g., *Geoxus, Irenomys*) in the sequence of this cave around 9.4–8 ka.

Pollen sequences at LL between 8 and 6 ka are indicative of a grass steppe developed with shrubs, which suggest edaphic conditions related to higher moisture availability than today (Prieto and Stutz, 1996). Westerlies became stronger after 6000 cal BP, allowing eastward spread of forest in the Andes (see Markgraf, 1993; Mancini et al., 2005). Perhaps related with these episodes is the high frequency of some elements associated with humid environments, such as *Chelemys* in the area around LL ca. 5.1 ka.

Steppe vegetation in CTI, indicated by a high representation of Gramineae, and Tubuliflorae is dominant at least since 6.2 ka (Heusser, 1993). This evidence is in line with the first records of steppe taxa such as *Eligmodontia* spp. and *G. leucoblephara*. In the Eastern foothills of the Andes, pollen evidence suggests a reduction in rainfall, especially during summer, between 8.9 and 5 ka with an increase in steppe elements (Markgraf, 1987; Markgraf et al., 2009). In the area around LL, a grass-shrub steppe transition dominated the community between 6 and 4 ka (Prieto and Stutz, 1996). At the same time, Monte elements (e.g., *Larrea, Chuquiraga* and *Prosopis*) appeared for the first time in the record, suggesting an increase in temperatures (Mancini et al., 2005).

Between 5 and 4 ka, proxy evidence suggests a transition toward present vegetation and climate patterns (Prieto and Stutz, 1996; Mancini et al., 2005). The floristic composition of the Andean forest is comparable to the modern mixed *N. dombeyi–A. chilensis* forest with annual precipitation >1500 mm and higher summer rains (Markgraf, 1984, 1993; Markgraf and Bianchi, 1999; Bianchi, 2000). In steppe areas, the transition between Patagonian and Monte-shrub steppe became established under semi-arid climatic conditions (Mancini et al., 2005). In accordance, Late Holocene small mammal communities in LL were enriched with the addition of *A. neocenus*, a typical Monte and Monte-Patagonia ecotone rodent.

Glacial advances occurred between 4.7 and 4.4 ka, 2.7 and 2.2 ka and during the Little Ice Age, indicating cooler and humid conditions during these periods (Mercer, 1976; Rabassa, 2008). There is no evidence of the impact of these advances in the faunas of CTI and LL, perhaps as a result of an inadequate resolution of these sequences. However, on a regional view, there is evidence of micromammal fluctuations related with some of these advances in the sites of Sarita IV (Teta et al., 2005) and Estancia Nahuel Huapi (Rebane, 2002).

The last centuries are characterized by a deep human impact, including changes in fire regimens, overgrazing, and desertification (e.g., Kitzberger and Veblen, 2003). European influence is registered between 0.2 and 0.6 ka at most sites in northwestern Patagonia (see Whitlock et al., 2006, 2007). Arrival of the European colonists occurred after 1850 (Kitzberger and Veblen, 1997), creating favorable conditions for some opportunistic taxa, such as *Calomys* spp., *Eligmodontia* spp., and *O. longicaudatus*, allowing their populations to increase in size and space (Pardiñas, 1999; Pardiñas et al., 2000; Teta et al., 2005).

3.5. Recent small mammal communities and human impact

The strong reworking of CTI and LL recent micromammalian communities, against those that characterized the entire Holocene, is a complex issue. The most dramatic change in CTI sequence occurred during the last century, involving drastic reduction of two largely dominant Holocene rodents, Ctenomys spp. and Euneomys spp., with an outstanding increment of O. longicaudatus (reaching values up to 73%). This latter species seems to be favoured by the introduction of the sweet briar (Rosa rubiginosa), an exotic shrub that this rodent largely uses as a refuge (Pearson, 1983) and food supply during autumn and winter (Pelliza Sbriller and Sepúlveda Palma, 2007). A similar restructuring, in time and magnitude, affected the LL assemblage, but involving other rodent species. There, only one drastic drop is observed, Ctenomys spp. At the same time, two elements associated with shrubby and relatively overgrazed environments, *Eligmodontia* spp. and *A. olivaceus*, became dominant. In addition, A. iniscatus increased in abundance and Calomys spp. appears in the pool of species. In both sequences, some dominant Holocene rodents reach modern communities without significant frequency variations, such as the cases of L. micropus in CTI and P. xanthopygus and R. auritus in LL. This fact, coupled with the variety of specific responses listed above, indicates that modern northwestern Patagonian small mammal communities are the result of individual specific responses to environmental alteration rather than replacements of species in the West-East gradient (Pardiñas et al., 2011).

As there is no significant climate fluctuations during the last century, at least in comparison with those recorded during the Holocene, the observed taxonomic restructuration of modern small mammal assemblages should be mainly attributed to human impact (Pardiñas, 1999; Pardiñas et al., 2000, 2012; Teta et al., 2005). Since the end of the 18th century, massive introduction of sheep, and to a lesser degree cows, horses and goats, characterized almost all Patagonian territory, with the highest numbers around 1940-1950 (Aagesen, 2000). Other human practices that grew exponentially were shrub removal by domestic fire from steppe and Monte habitats; forest clearance by cutting or burning; and wood extraction in Forest environments (Veblen and Markgraf, 1988). From the beginning of the past century, another anthropogenic element was added with the introduction of hares (Lepus europaeus), rabbits (Oryctolagus cuniculus), and exotic shrubs (e.g., R. rubiginosa). Finally, the incorporation of horses by Patagonian aboriginals between the 18th and 19th century definitively changed the fire regimes (e.g., Veblen et al., 1999; Whitlock et al., 2006).

Based on the present evidence, human activities probably had a negative impact on *Euneomys* spp. populations, but the specific moment of this impact is unknown. However, it is clear that this rodent became a marginal element in Subandean northwestern Patagonian environments after 10,000 (or more) years of predominance. More or less persuasive hypotheses can be advanced in order to explain other observed specific shifts. Shrub expansion and grassland reduction produced by cattle overgrazing and the introduction of some exotic shrubs favored increments of A. olivaceus, A. iniscatus, O. longicaudatus, and Eligmodontia spp. (see Pearson, 1983; Monjeau, 1989). Soil compaction by sheep trampling reduced subterranean rodents (Ctenomys). However, these explanations do not consider intra- and inter-specific relationships, such as competition or predation pressure. Why does Euneomys spp. remain extremely abundant in western Santa Cruz environments despite the sheep introduced there during the last century? Why did Loxodontomys drop in western Santa Cruz environments (cf. Pardiñas, 1998) but remain basically stable in northwestern Patagonia? Both species were co-dominant during almost all the Holocene in very different geographic locations along western Patagonia. These are many and complex questions considering the evidence currently at hand; more fossil and recent samples need to be studied in Patagonia.

4. Final considerations

Simonetti and Rau (1989) concluded that there were no changes between Late Pleistocene and modern communities, based on the results of the study of a fossil rodent sample from Cueva del Milodón, Southern Patagonia. Pearson and Pearson (1993) highlighted the community persistence throughout the Holocene, from the evaluation of the CTI micromammal sequence. Despite these similar conclusions, both studies contributed to generate a partially inaccurate conception on the real value of Quaternary micromammal assemblages as a tool in paleoenvironmental reconstruction. Community stability is not necessarily a mirror of lack of environmental change. Clearly, micromammals in Quaternary evolution are a proxy data of gross resolution in comparison to more detailed results from pollen, diatoms, tree-rings, or glacial sediments (e.g., Páez et al., 2001). However, several advantages such as the local provenance, the comparative low cost of data collection and analysis can be drawn in favor of the study of micromammal assemblages. In addition, for many arid regions this kind of data is almost the only information in paleoclimate archive available (Pardiñas and Teta, 2008; Ortiz et al., 2012; Fernández et al., 2012).

Perhaps the more interesting point achieved from the study of both CTI and LL sequences is that the taxonomic structure of recent small mammal communities in northwestern Patagonia is the result of processes exerted in the last century. The observed changes include an alteration of dominance relationships with a variety of specific responses, from virtual extirpations (e.g., *Ctenomys* spp., *Euneomys* spp.) to higher representations (e.g., *A. olivaceus, Eligmodontia* spp., *O. longicaudatus*), very recent invasions (*A. iniscatus, Calomys* spp.), and probable regional extinctions (e.g., *Lestodelphys, Notiomys*). All these pieces form a complex and poorly resolved puzzle, hard to assess in view of the fragmentary and condensed record of most of the available paleoclimatic archives.

The results obtained in this contribution strongly indicate that the most dramatic change suffered by micromammal communities in northwestern Patagonia occurred during very recent times. Regrettably, in Patagonia there was not enough trapping effort comparable to that carried out in Yosemite National Park at the beginning of the past century, replication of which permitted assessment of the impact of human induced climate change on small mammal communities (Moritz et al., 2008). To partly fill this lacuna, detailed study of short-term micromammal sequences, particularly those produced solely by owl trophic activities, seems to be a promising and informative method (e.g., Bilney et al., 2010; Terry, 2010). This kind of deposit appears to be widespread in northwestern Patagonia (cf. Pearson and Christie, 1993; Rebane, 2002), as well as in other portions of this vast territory (cf. Pardiñas, 1999; Pardiñas et al., 2000; Udrizar Sauthier, 2009), and surely encloses useful insights to understand the fundamental changes suffered by the small mammal communities and environments during the last century.

Acknowledgments

This contribution incorporates data and conclusions achieved during the concretion of the doctoral thesis of UFJP under the advisor of Eduardo P. Tonni and the late Oliver P. Pearson. The study of LL material and the additional samples of CTI were possible thanks to Eduardo Crivelli Montero, Mabel Fernández, and Agustín Cordero. Anahí Formoso, Erika Cuéllar, Joaquín Pardiñas, Fabián Llanos, Gustavo García, Daniel Udrizar Sauthier, Darío Podestá,

Sebastián Cirignoli, and Agustín Cordero, participated during field work and/or laboratory activities or kindly provided samples. More recently, the work in progress of M. Tammone expanded our perception of landscape and rodents in northwestern Patagonia. This research was funded by CONICET and Agencia PICT 32405 and PICT 2008-0547 (both to UFJP). Oliver Pearson's field notes were accessed at the Museum of Vertebrate Zoology Library in a short trip of the senior author sponsored by Jim Patton. Finally, Pancho Prevosti, Luis Borrero, and Fabiana Martin assisted us with a kindly invitation to contribute to this volume and many years of friendship. To the mentioned persons and institutions, our deep gratitude.

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