



Last glacial maximum environments in northwestern Patagonia revealed by fossil small mammals



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ABSTRACT

Comparisons of historical and modern assemblages of mammals can yield important insights into patterns and processes of environmental change. Here, we present the first analyses of small mammal assemblages present in northern Patagonia during the last glacial maximum (LGM). Using remains obtained from owl pellets excavated from an archeological cave site (Arroyo Corral I, levels VII–V, carbon dates of 22,400–21,530 cal yr BP), we generate estimates of the minimum number of individuals for all species detected; these estimates, in turn are used to determine relative species abundances. Comparisons of these data with similar analyses of small mammal remains obtained from a second archeological site (AColl, levels IV–V, carbon dates of 10,010–9220 cal yr BP) as well as from modern owl pellets reveal pronounced changes in relative species abundance since the LGM. In particular, *Euneomys chinchilloides* and *Ctenomys sociabilis* – the predominant species during the LGM – declined markedly, suggesting a change from open, bare habitat punctuated by patches of wet meadows and shrubs to the more densely vegetated mosaic of ecotone habitats found in this region today. These data provide important new insights into the environmental changes that have occurred in northern Patagonia over the last 20,000 years.

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Introduction

Reconstructing historical faunas can generate important insights into patterns and processes of evolutionary change. In addition to revealing temporal changes in the compositions of specific biotas, such reconstructions can be used to draw inferences regarding associated patterns of habitat and climate change. For small bodied mammals, analyses of bones and teeth deposited around owl or raptor roosts represent a particularly direct means of characterizing historical assemblages (Andrews, 1990; Stahl, 1996). Information obtained from such deposits can be used to document temporal changes in multiple aspects of a species' biology, including relative abundance (Grayson, 1983; Terry, 2010a, 2010b), body size (Barnosky, 1994; Hadly et al., 1998), and genetic variability (Hadly et al., 1998; Chan et al., 2005). In conjunction with data regarding a species' current ecology, such analyses can be used to draw inferences regarding associated environmental changes (Barnosky et al., 1996; Hadly, 1996) and, potentially, the causes of biotic change over time.

In South America, glacial cycles are thought to have been critical in shaping habitats and associated biotas (Lessa et al., 2003, 2010), with multiple advances and retreats of ice sheets causing pronounced changes

over relatively short periods of time (Heusser et al., 2006). The last glacial maximum (LGM) at the end of the Pleistocene (~23,000–19,000 yr) was the most recent significant expansion of ice on a global scale. In northern Patagonia, the geological nature of this event has been well characterized based on current landforms and other evidence of glacial activity (Porter, 1981; Hulton et al., 2002; Rabassa, 2008; Rabassa et al., 2011). In contrast, the impact of the LGM on the flora and fauna of this region is less well understood, with inferences about paleoenvironments drawn primarily from phylogeographic studies of extant taxa (Turchetto-Zolet et al., 2013). More direct characterizations of biotic assemblages based on fossil data are almost non-existent, with available information limited primarily to analyses of insects and pollen from south-central Chile (e.g., Hoganson and Ashworth, 1992; Moreno, 1997; Heusser, 2003).

With regard to small mammals, a number of Patagonian fossil assemblages have been collected, primarily in archeological contexts (Pearson and Pearson, 1993; Teta et al., 2005; Fernández et al., 2012; Pardiñas and Teta, 2013). Most of these collections, however, are restricted to the Holocene; although a few cover the Pleistocene–Holocene transition, none extend to the LGM. Indeed, the oldest known small mammal assemblage recovered from northern Patagonia (El Trébol archeological site, Neuquén Province, Argentina) dates to only 10,570 ± 130 ¹⁴C yr BP (AA-65707) (Hajduk et al., 2004, 2006) and thus does not encompass the last major glacial advance. As a result, the small mammal faunas of this region during the LGM are unknown

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(Tonni and Carlini, 2008; Pardiñas et al., 2011), precluding comparisons of historic and modern assemblages to assess biotic changes over the last ~20,000 years.

Here, we studied a fossil assemblage of Patagonian small mammals from the LGM. The materials examined are from the Río Limay Valley in the Nahuel Huapi region of northwestern Argentine Patagonia, an area that has been the subject of considerable research regarding modern small mammals (Pearson and Pearson, 1982; Pearson, 1984; Monjeau et al., 1997; Pardiñas et al., 2003). Using materials collected from three cave sites in southern Neuquén and Río Negro Provinces, we characterize the taxonomic composition and relative species abundances of the small mammal faunas present at these locations during the LGM. Through comparisons of these data with information regarding the modern mammals of this region, we quantify changes in the vertebrates of this region since the LGM and, based on the ecologies of extant taxa, use these analyses to explore apparent habitat changes over the same time period. In addition to providing the first characterization of a Patagonian small mammal assemblage from the LGM, our data provide new insights into patterns of environmental change in this region over the past ~20,000 years.

Methods

Fossil samples

Small mammal remains were retrieved from the archeological site Arroyo Corral I (ACol) (Arias et al., 2013; 40°55'52"S, 71°03'19"W [WGS84], 844 m.a.s.l.), located on Estancia La Lonja in Parque Nacional Nahuel Huapi (PNNH), Neuquén Province, Argentina (Fig. 1). The site, which overlooks the Río Limay, consists of a rocky cave composed of two well-developed caverns, each measuring ca. 20 m by 14 m, with a ceiling height of ca. 3 m (Fig. 2). The surrounding habitat consists

primarily of precordilleran steppe representing the ecotone between semiarid Patagonian steppe and Andean *Nothofagus* forests. Vegetation in the area is dominated by small shrubs (*Mulinum spinosum*, *Acaena splendens*) and bunch grasses (*Festuca pallescens*, *Stipa speciosa*) and is punctuated by isolated groves of the evergreen cypress *Austrocedrus chilensis* (León et al., 1998; Bran, 2000).

During the austral summer of 2006, a 2-m by 2-m pit was excavated at ACol (Fig. 2). Digging was completed using hand-held trowels following natural stratigraphic boundaries. Excavation extended to a depth of 280 cm before reaching bedrock. Seven sedimentary levels (labeled I to VII) were identified. All soil removed was sieved in the field using a screen with a 2-mm mesh size. Material collected from each stratigraphic level was placed in a plastic bag and transported to the archeological laboratory in the Museo de la Patagonia in San Carlos de Bariloche (Río Negro Province, Argentina) for final separation and sorting of mammal remains.

Chronology and taphonomy

The small mammal assemblages examined were collected from the three basal levels (V to VII) of the ACol stratigraphic sequence. Radiocarbon dating performed by accelerator mass spectrometry (AMS) on bone collagen from specimens of Mylodontinae and *Lama guanicoe* contained in these levels generated the following estimates of stratigraphic ages: (1 = AMS Laboratory, University of Arizona; 2 = Oxford Radiocarbon Accelerator Unit, University of Oxford; 2-sigma calibration interval)

Level V: 21,267–19,998 cal yr BP [18,700 ± 260 ¹⁴C age BP (AA-75674)¹]

Level VII: 21,886–21,203 cal yr BP [19,520 ± 100 ¹⁴C yr BP (OxA-19478)²]

22,108–20,754 cal yr BP [19,410 ± 280 ¹⁴C age BP (AA-75675)¹]

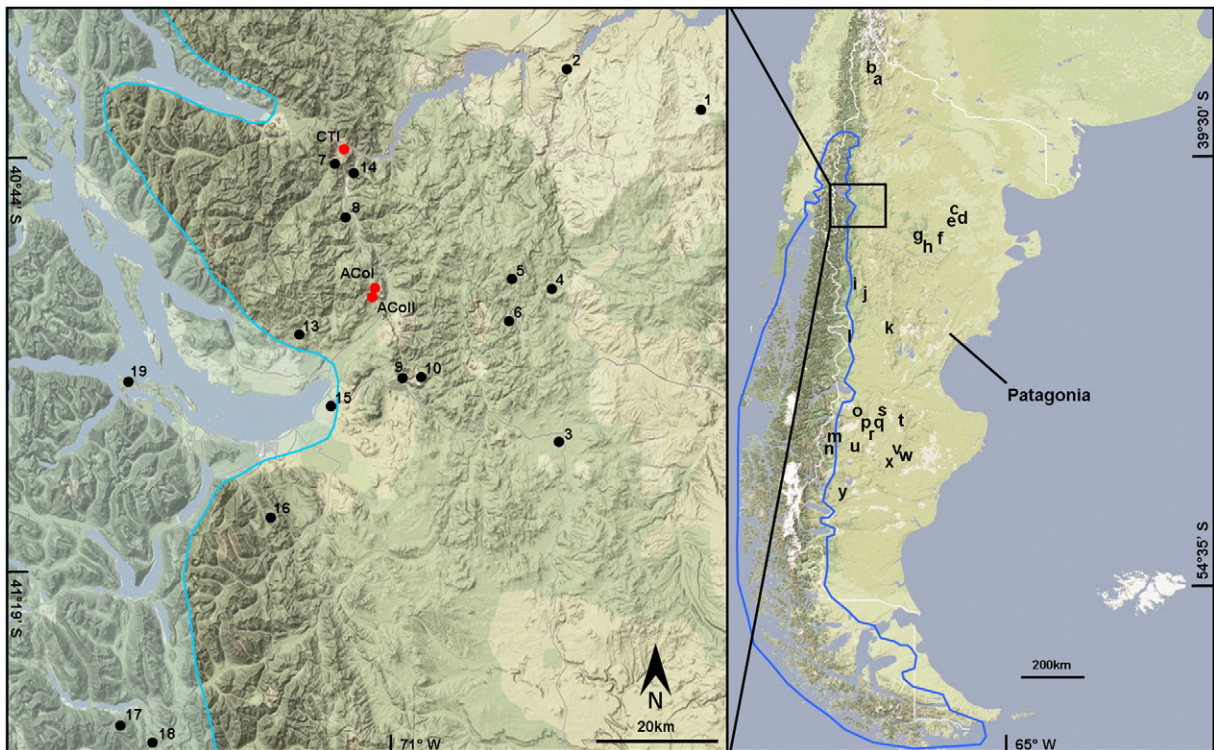


Figure 1. Map of the study area in northern Patagonia. In (A), a detailed map of the Limay Valley region is shown; this area includes the ACol, AColI, and CTI sites at which fossil material was collected (red dots) as well as the 19 locations at which modern owl pellets were collected (black dots). In (B), a larger portion of Patagonia is shown, with the 25 locations at which modern owl pellets were collected noted. The blue line indicates the estimated limit of ice sheets during the LGM.

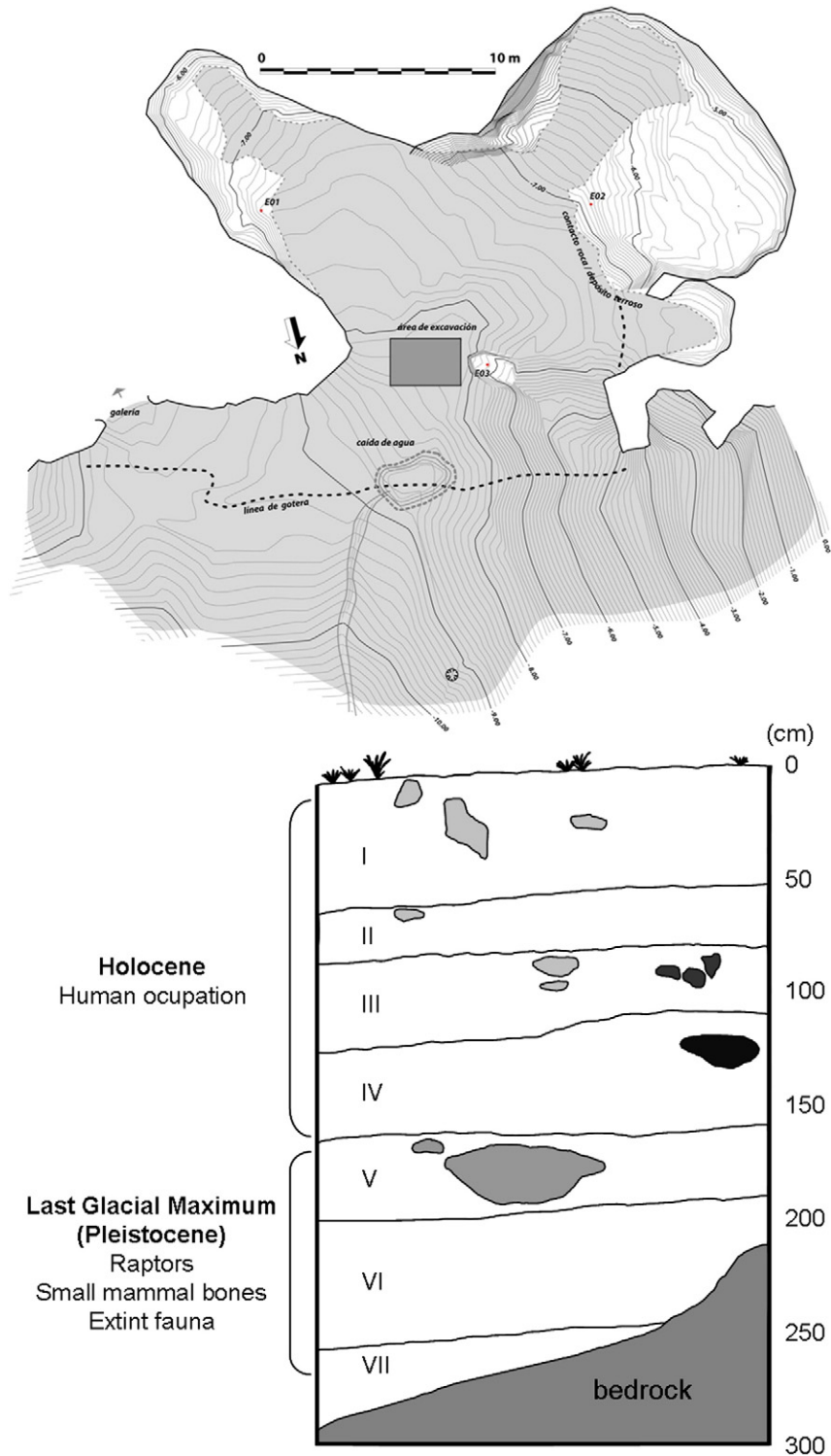


Figure 2. Map of the Arroyo Corral I collection site. In the upper panel, the location of the excavation site (gray rectangle) within the cave is indicated. Topography and imaging: Luis C. Teira Mayolini. In the lower panel, the stratigraphic sequence of the excavation pit is depicted.

Date calibration was accomplished using the IntCal13 calibration curve (Hogg et al., 2013) with the OxCal4.2 calibration software package (Bronk Ramsey, 2009). These estimates of stratigraphic age are concordant with the timing of the last glacial maximum in southern South America (Porter, 1981). No evidence of human occupation was detected at these levels of the cave. Given both the relatively short time span encompassed by these samples (~1000 years) and the absence of pronounced differences in the matrix recovered, and in the source of

sample deposition (see below) from these strata, we pooled material recovered from levels V–VII for subsequent analyses.

Small mammal remains from ACoI consisted of cranial, dental, and postcranial material. The taphonomy at the site was characterized using two approaches. First, bones and teeth were inspected using a hand-held magnifying glass to detect evidence of digestion and to determine the degree of fragmentation of each specimen. The breakage pattern of the bones examined, the low percentage of broken post-

cranial material, and the limited corrosion (<1%) of long bones (e.g., humerus, femur) and teeth were all consistent with an avian predator as the main agent responsible for small mammal sample deposition (Andrews, 1990; Stahl, 1996); this interpretation was supported by the discovery of numerous in-situ owl pellets during our excavations. Second, the relative abundances of nine skeletal elements (mandible, maxilla, scapula, humerus, radius, pelvis, femur, tibia, and calcaneus) were quantified for each stratigraphic level using the following formula: $N_i / (E_i \times MNI) \times 100$, where N_i is the number of each element in the sample, E_i is the expected number of each element per individual, and MNI is the minimum number of individuals (Andrews, 1990). Relative abundances of these skeletal elements (Fig. 3) indicate that the taphonomic agent was the same for all three stratigraphic levels, with the high abundances of cranial elements, humeri and femora being consistent with deposition by owls (Terry, 2007).

Given these lines of evidence, we conclude that the small mammal remains recovered from ACoI were deposited primarily – if not exclusively – by owls. In Patagonia, only two owl species use caves and are capable of producing such bone deposits – the Barn Owl (*Tyto alba*) and the Magellanic Horned Owl (*Bubo magellanicus*). The Barn Owl is the most common and most widely distributed owl in Patagonia, where it roosts primarily in caves (Travaini et al., 1997; Pardiñas and Cirignoli, 2002) and has been shown to be responsible for the deposition of small mammal bones at numerous archeological sites (Pearson and Pearson, 1993; Pardiñas, 1999a, 1999b; Teta et al., 2005). In contrast, the Magellanic Horned Owl nests mainly in open areas and uses caves only occasionally as resting sites (Trejo et al., 2005a). Thus, although we expect that *T. alba* was the primary agent of bone accumulation at ACoI, we cannot rule out potential contributions by *B. magellanicus*. However, even if both species had occupied the cave at different points in time, we do not expect this variation to have impacted our paleoenvironmental reconstructions samples due to the marked similarity in hunting behavior and associated large overlap in diet between Barn and Horned Owls (Trejo et al., 2005b; Trejo, 2006).

Additional fossil samples

Although our study focused on material deposited at ACoI, we also examined small mammal remains obtained from two other archeological sites in the vicinity of the Limay Valley. The first of these, Arroyo Corral II (ACoII), is a distinct cave located ~100 m uphill from ACoI. Excavation of ACoII is ongoing, but small mammal remains obtained from levels IV and V of this site (the oldest levels available) were examined using the methods described above. AMS dating of a bone from an unidentified large mammal placed level IV at 10,007–9294 cal yr BP [10,020 ± 96 ¹⁴C age BP (AA-75677)] and dating of a rodent (*Ctenomys*) mandible placed level V at 9802–9216 cal yr BP [9890 ± 97 ¹⁴C age BP (AA-100200)]. Thus, samples from this site were deposited during the early Holocene, most likely due to a combination of human activity and owl

predation. The second site, Cueva Trafal I (CTI) is a well-characterized archeological dig located about 25 km north of ACoI (Crivelli Montero et al., 1993; Pearson and Pearson, 1993). We examined the data set for small mammals from CTI provided in Pardiñas and Teta (2013). Based on dates published by Crivelli Montero et al. (1993), this material ranged from the early (9285 ± 105 ¹⁴C yr BP, LP-62) to the late (2230 ± 40 ¹⁴C yr BP, LJ-5130) Holocene. Thus, collectively, the three cave sites examined span the last ~20,000 years.

Modern samples

To provide an appropriate temporal comparison, we collected fresh owl pellets from 19 sites in the Limay region. Samples were collected within a ~50-km radius of ACoI to allow characterization of the small mammal fauna in the vicinity of our historical cave sites (Fig. 1). We assigned a habitat type to each modern locality following the scheme of León et al. (1998), with habitat types assessed visually at the time of sample collection (Table 2). Owl pellets were recovered from beneath nests and roost sites; based on feathers found in nests as well as direct observations of nest and roost sites, pellets were attributed to *T. alba*. To provide a larger, regional-scale perspective on the small mammal fauna potentially represented in LGM assemblages, we also analyzed remains contained in 25 modern owl pellet samples drawn from a large (>300 samples; Formoso, 2013) unpublished database covering most of Argentine Patagonian (Fig. 1).

Taxonomy and quantification

To determine the number of taxa present in a sample (i.e., species richness), cranial and dental remains were identified using dichotomous keys (Pearson, 1995; Fernández et al., 2011) as well as comparisons with reference specimens housed in the Colección de Mamíferos del Centro Nacional Patagónico (CENPAT-CONICET; Puerto Madryn, Argentina). The taxonomy employed here follows Musser and Carleton (2005) and Pardiñas et al. (2011). To estimate a species' relative abundance, the minimum number of individuals (MNI) present in a sample was calculated using cranial (mandibles, maxillae) and dental remains (Grayson, 1984), a second abundance estimator (NISF) was calculated but not used in the analysis; estimates were based on the most abundant of these anatomical elements, with bilateral symmetry (i.e., two elements per individual) taken into account. MNI was calculated for each of the 3 (V–VII) stratigraphic levels from ACoI and for each modern pellet-derived assemblage. To standardize MNI values calculated for each taxon, MNI was divided by the total number of individuals (all taxa combined) in the sample, generating estimates of the relative abundance of each taxon considered. Due to the marked variation in samples sizes for the different fossil levels, rarefaction curves (Colwell et al., 2004) were calculated for each level in order to assess reliability of our estimates of richness and relative abundance.

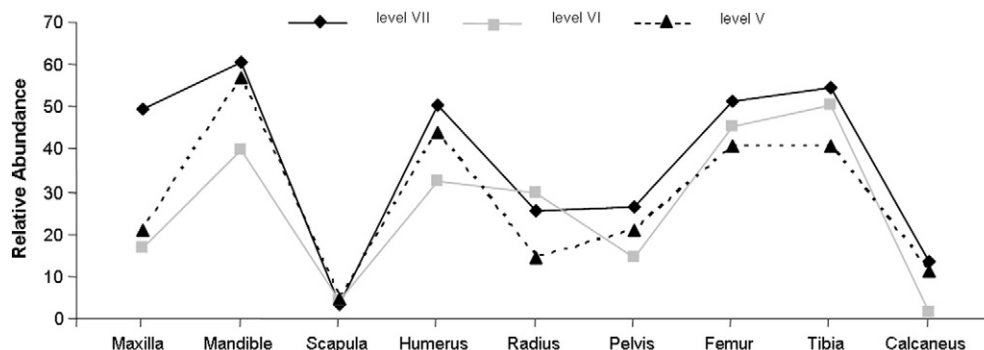


Figure 3. Relative abundance of the nine skeletal elements at the three LGM levels.

Table 1
Estimates of the minimum number of individuals (MNI) by taxon for three stratigraphic levels excavated at Arroyo Corral I (ACol) in southern Neuquén Province, Argentina. Carbon dates for these levels are shown and correspond to the last glacial maximum (LGM). The same information is presented for early Holocene samples collected from the nearby Arroyo Corral II (ACoII) as well as modern samples collected at ACoI. In brackets is the number of identified specimens (NISF).

Site	Level	¹⁴ C age BP	Abrothrix longipilis	Abrothrix olivaceus	Chelemys macronyx	Ctenomys sociabilis	Eligmodontia morganii	Eumomys chinchilloides	Irenomys tarsalis	Loxodontomys micropus	Microcavia australis	Oligoryzomys longicaudatus	Phyllotis xanthopygus	Reithrodontomys auritus	Total MNI	Total NISF	# species
ACoI	#VII	19,410 ± 280	0	2 (2)	7 (13)	6 (6)	0	36 (107)	0	0	0	0	6 (7)	0	57	135	5
		19,520 ± 100															
ACoI	#VI	No date	1 (1)	1 (1)	1 (1)	5 (7)	0	10 (16)	0	0	0	0	1 (1)	0	19	29	6
ACoI	#V	18,700 ± 260	0	0	0	4 (5)	1 (1)	8 (12)	0	1 (1)	0	0	1 (1)	0	15	20	5
ACoII	#IV	9890 ± 97	2 (2)	1 (1)	1 (1)	64 (134)	0	7 (11)	0	9 (15)	7 (10)	0	1 (2)	10 (20)	102	196	9
		10,020 ± 96															
ACoII	Modern		33 (73)	23 (57)	8 (22)	7 (13)	10 (28)	3 (7)	18 (45)	33 (70)	0	22 (61)	8 (19)	36 (122)	201	518	11

Community structure analyses

To explore relationships between relative abundance estimates for fossil and modern taxa, Non-Metric Multidimensional Scaling (NMDS) analyses were performed (Taguchi and Oono, 2005). These analyses generated a Bray–Curtis statistic calculated from matrices of per-species abundances (%MNI) arranged (1) per-stratigraphic level for fossil assemblages and (2) per-locality for modern assemblages. To determine if species composition differed between time periods or between sampling localities within time periods, an Analysis of Similarities (ANOSIM; Clarke, 1993) was conducted using the Bray–Curtis statistics derived from our NMDS analyses. ANOSIM produces a statistic *R*, large values of which (i.e., *R* ~1) signify dissimilarity between groups. Pairwise ANOSIMs completed for all temporal and spatial combinations of data points were used as a post-hoc test of significance for individual *R* values, with a sequential Bonferroni test (Rice, 1989) conducted to determine appropriate alpha values. Finally, Similarities Percentage Analysis (SIMPER; Clarke, 1993) was used to identify the taxa contributing to significant differences between time periods or sampling localities. All analyses were conducted using the computer package PAST 1.81 (Hammer et al., 2001).

Paleoenvironmental analyses

Analyses of small mammal remains recovered from owl pellets are a relatively standard method for comparing faunal assemblages across time periods (Pearson and Pearson, 1993; Andrade and Teta, 2003; Fernández et al., 2012). Two attributes of owl biology make such samples particularly appropriate. First, the remains found in owl pellets are better preserved than those left by other predators and, second, the high roost fidelity displayed by many owl species leads to accumulation (with eventual fossilization) of extensive collections of material over time (Andrews, 1990). *T. alba* – the species most likely to have produced the deposits analyzed here – has been shown to prey primarily on small mammals; the specific prey items taken are determined by the habitats present with the ~5 km hunting radius of these animals, with no selection for specific prey species known to occur (Taylor, 1994; Pardiñas et al., 2003; Trejo and Lambertucci, 2007). As a result, assemblages of small mammal remains collected by owls are thought to provide useful indicators of the habitat types and thus the environments present at the time that predation occurred (e.g., Pearson and Pearson, 1993; Pardiñas, 1999a; Andrade and Teta, 2003; Teta et al., 2005; Trejo and Lambertucci, 2007; Pardiñas and Teta, 2008; Fernández et al., 2012). Thus, based on information regarding the current habitat preferences of the small mammals of northern Patagonia (Pearson and Pearson, 1982; Pearson, 1983, 1984, 1987, 1995; Pardiñas and Teta, 2013), we used comparisons of relative abundances in historical and modern assemblages (Overpeck et al., 1985) to draw inferences regarding the paleoenvironments of the study region.

Results

Temporal comparisons of assemblages at ACoI

A total of 181 cranial and dental remains from LGM small mammals were recovered from levels VII to V at ACoI. All remains were identified to species and consisted of either caviomorph or cricetid rodents. The total minimum number of individuals (MNI) was 91 and represented 8 species; 7 sigmodontines and 1 ctenomyd (Fig. 4 and Table 1). Rarefaction analyses revealed that although the species accumulation curve for level VII reached an asymptote, the curves for levels V and VI did not (Fig. 5). This suggests that while data from level VII provide a good representation of species richness, data from levels V and VI may have been biased in their estimates of species richness, most likely due to small sample sizes for these strata. When data from all 3 levels were pooled for analysis, the resulting rarefaction curve reached an

Table 2

Estimated MNIs for small mammal taxa found in modern owl pellets collected from 19 localities in Patagonia. NISP numbers on Supplementary Table 4.

#	Locality	Habitat	<i>Dromiciops gliroides</i>	<i>Abrothrix longipilis</i>	<i>Abrothrix olivaceus</i>	<i>Akodon iniscatus</i>	<i>Akodon neocenus</i>	<i>Chelemys macronyx</i>	<i>Ctenomys</i> spp.	<i>Eligmodontia</i> spp.	<i>Euneomys chinchilloides</i>	<i>Galea leucoblephara</i>
1	Cañadón A° Fuquelen	Arid steppe	0	0	15	0	0	0	29	28	0	0
2	Cerro Castillo	Arid steppe	0	1	6	0	7	0	38	104	0	1
3	Estancia Pilcañeu	Arid steppe	0	11	74	0	0	0	44	61	18	0
4	Paso de Los Molles	Arid steppe	0	1	36	4	0	0	15	10	0	0
5	Pipilcura	Arid steppe	0	19	15	0	0	7	27	1	4	0
6	Cooperativa Escuela	Arid steppe	0	19	51	0	0	3	14	25	12	0
7	Valle Encantado	Grassy steppe	0	56	5	0	0	7	17	23	0	0
8	La Lipela	Grassy steppe	0	119	11	0	0	0	13	14	3	0
9	San Ramón	Grassy steppe	0	36	15	0	0	3	15	21	0	0
10	Laguna Los Juncos	Grassy steppe	0	25	12	0	0	1	10	8	0	0
11	Corral II (modern)	Grassy steppe	0	33	23	0	0	8	7	10	3	0
12	Cueva Trafal I (modern)	Ecotone	0	28	7	0	0	8	7	8	0	0
13	Cliff Jones	Ecotone	0	143	24	0	0	12	9	6	11	0
14	Cueva del Caballo	Ecotone	0	170	59	0	0	6	44	62	5	0
15	Cerro Leones	Ecotone	0	566	393	0	0	27	50	169	23	0
16	Chalhuaco	Ecotone	3	59	1	0	0	44	20	6	3	0
17	Lago Steffen	Forest	0	7	36	0	0	1	0	0	0	0
18	Cabaña Cacique Foyel	Forest	0	6	11	0	0	0	0	0	0	0
19	Llao-Llao	Forest	0	5	0	0	0	0	0	0	0	0

asymptote (Fig. 5) and thus this pooled data set was used for further analyses of faunal composition. In all 3 levels examined as well as in the pooled data set, assemblages were dominated by the rock-dwelling sigmodontine *Euneomys chinchilloides* (59% of MNI), followed by the subterranean *Ctenomys sociabilis* (16.4%; Fig. 6).

Comparisons of the small mammal assemblages from ACOI and ACOII revealed that all taxa detected during the LGM were also present in modern samples but that relative species abundance has changed markedly over time. Total species richness ($N = 8$ species) was lowest during the LGM and highest ($N = 11$ species) in the modern sample (Figs. 4 and 5); this change was due primarily to the addition of *Reithrodon auritus* during the early Holocene and the addition of *Irenomys tarsalis* and *Oligoryzomys longicaudatus* in modern samples. With regard to relative abundances, the most conspicuous changes were the decrease in frequency of *E. chinchilloides* and *C. sociabilis* from the LGM to today. More generally, modern samples were dominated by taxa (*Abrothrix longipilis*, *Loxodontomys micropus*, *R. auritus*) that had low abundances or that were absent during the LGM. Samples from the early Holocene contained the only occurrences of *Microcavia australis* and were distinguished by the extreme prevalence of *C. sociabilis*, both of which may reflect taphonomic biases related to human consumption of these rodents.

Spatial comparisons across the Limay region

Expanding the spatial scale of our comparisons to include samples from CTI revealed that *E. chinchilloides* was also the dominant species at this location. Thus, collectively, data from ACOI, ACOII, and CTI suggest that this animal was common (23–63% of total MNI) in the Limay region during much of the Pleistocene–Holocene (Table 1, Fig. 6). Samples from CTI and ACOI were also similar in that two species specializing on forest habitat, *I. tarsalis* and *Geoxus valdivianus* were absent before ~9 ka, as was *O. longicaudatus*, which occurs in moist, brushy habitats (Table 1, Fig. 6). The same 3 species were also absent in the early Holocene material from ACOII (Table 1, Fig. 6). The absence of these species from the fossil assemblages examined suggests that dry, open habitats characterized this region during the late Pleistocene.

Comparison of these fossil assemblages with data from modern owl pellets collected in the Limay region revealed that the small mammal fauna of this area has changed markedly since the LGM. NMDS ordination analyses revealed no relationship between the fossil and modern samples examined, with the fossil LGM assemblage from ACOI being clearly distinct from CTI, ACOII and the modern assemblage (Fig. 7). Based on these results, analyses of similarity (ANOSIM) were conducted

by dividing our data into 4 temporal categories – LGM, ACOI 10 ka, CTI, and modern – with the modern samples further subdivided by habitat type (Fig. 7). ANOSIM results indicated significant differences in species composition and abundance among these categories ($R = 0.880$, $P < 0.001$). Post-hoc pairwise comparisons confirmed significant differences among all of these assemblages as well as among the different modern habitat types (Supplementary Table 2). SIMPER analyses identified *E. chinchilloides* as the primary taxon underlying these differences, followed by *O. longicaudatus* (Supplementary Table 3). As noted above, *E. chinchilloides* was abundant in fossil assemblages while *O. longicaudatus* is an abundant component of modern assemblages.

Comparisons across Patagonia

Given the prevalence of *E. chinchilloides* in the LGM assemblage from ACOI, we searched an unpublished database of small mammal remains obtained from owl pellets collected in Patagonia (Colección de egagrópilas del Centro Nacional Patagónico; Formoso, 2013) to identify modern assemblages containing >30% *E. chinchilloides* (total MNI >100). This search resulted in 25 samples for analysis (Supplementary Table 1). NMDS ordination revealed no conspicuous association between ACOI and any of the 25 modern samples considered (Fig. 7). Similarity was greatest (Bray–Curtis index = 0.7856) between ACOI and a sample from Cajón Grande Curi Leuvu in Neuquén Province. This site is located ~500 km north of ACOI at an elevation of 1885 m.a.s.l., which is above the current treeline for that portion of the Andes Mountains.

Paleoenvironmental interpretations

Assuming that the habitat requirements of small mammals in Patagonia have not changed substantially over the last ~20,000 years, the above data allow us to draw several inferences regarding the habitats present at ACOI during the LGM. First, the predominance of *E. chinchilloides* in the ACOI assemblage coupled with the presence of *P. xanthophygus* in these samples suggests an open, relatively barren rocky habitat. This hypothesis is also consistent with the similarity between the ACOI assemblage and the composition of owl pellets collected at Cajón Grande Curi Leuvu. Second, the occurrence of *C. sociabilis* and *Chelemys macronyx* are suggestive of the presence of patches of mesic habitat, perhaps associated with glacial runoff or other small waterways. Third, the absence of forest-dwelling taxa (e.g., *I. tarsalis* and *G. valdivianus*) from ACOI suggests an absence of extensive tree cover. Collectively, these inferences

<i>Geoxus valdivianus</i>	<i>Irenomys tarsalis</i>	<i>Lestodelphys halli</i>	<i>Loxodontomys micropus</i>	<i>Microcavia australis</i>	<i>Octodon bridgesii</i>	<i>Oligoryzomys longicaudatus</i>	<i>Phyllotis xanthopygus</i>	<i>Reithrodon auritus</i>	<i>Thylamys pallidior</i>	TOTAL	# species	LS	LW	Reference
0	0	8	0	0	0	2	7	26	2	117	8	40° 40'	70° 25'	(1)
0	0	5	2	0	0	5	29	58	0	256	11	40° 35'	70° 40'	(2)
0	0	11	5	0	0	0	4	111	0	339	9	41° 08'	70° 41'	(1)
0	0	2	0	0	0	0	1	20	0	89	7	40° 55'	70° 43'	(1)
1	0	0	27	0	0	1	2	31	0	135	11	40° 54'	70° 48'	(3)
0	0	0	19	0	0	0	8	18	0	169	9	40° 58'	70° 48'	(3)
5	19	0	69	0	0	74	11	2	0	288	11	40° 45'	71° 08'	(3)
0	6	0	96	0	0	64	2	31	0	359	10	40° 49'	71° 06'	(3)
2	2	0	22	0	0	36	16	72	0	240	11	41° 03'	70° 59'	(3)
0	0	0	51	0	0	6	1	54	0	168	9	41° 03'	71° 00'	(4)
0	18	0	33	0	0	22	8	36	0	201	11	40° 56'	71° 03'	This paper
7	0	0	18	0	0	115	3	2	0	203	10	40° 43'	71° 07'	This paper
19	31	0	271	0	7	187	4	53	0	777	13	40° 59'	71° 13'	This paper
4	25	0	95	1	2	242	19	2	0	736	14	40° 45'	71° 05'	This paper
18	20	0	621	0	0	508	19	361	0	2775	12	41° 04'	71° 08'	(4)
18	0	0	84	0	0	42	2	6	0	288	12	41° 15'	71° 16'	(3)
2	7	0	19	0	0	29	0	0	0	101	7	41° 32'	71° 35'	(5)
1	6	0	21	0	0	38	0	0	0	83	6	41° 35'	71° 31'	(5)
1	9	0	35	0	0	82	0	0	0	132	5	41° 03'	71° 34'	This paper

suggest that during the LGM, the area around ACoI contained (1) more barren, rocky habitat and open grasslands punctuated by mesic areas of glacial runoff; but (2) less shrubland and fewer stands of trees than occur at this site today.

Discussion and conclusions

Comparisons of historical and modern faunas can generate important insights into patterns of environmental change (e.g., Pearson, 1987; Avery, 1992; Blois et al., 2010; Ortiz et al., 2011; Terry et al., 2011; Fernández et al., 2012; Schmitt and Lupo, 2012). Assemblages of small mammal are particularly useful for this purpose because, in contrast to larger-bodied species, these animals are often of local derivation and have relatively narrow microhabitat requirements (e.g., Stahl, 1996; Terry, 2010a, 2010b). As a result, small mammal remains can provide detailed information regarding environmental conditions at specific localities. Our analyses of cranial and dental remains recovered from owl pellets revealed significant changes in the composition of the small mammal fauna in the Limay Valley region of Patagonia over the past ~20,000 years. In general, both species richness and evenness have increased since the LGM; accordingly, the relative abundances of some species have changed markedly during this period. Analyses of modern owl pellets collected throughout northern Patagonia revealed no pronounced geographic variation among the small mammal faunas contained in these samples, suggesting that the differences evident in the Limay Valley region are due primarily to temporal, rather than spatial, variation in small mammal assemblages. Extrapolating from these findings (in particular, changes in the relative abundance of several species), our data suggest that the habitats surrounding the ACoI study site have changed markedly since the LGM.

Reconstructing LGM environments

The composition of the LGM fauna at ACoI suggests a largely open, rocky environment punctuated by moister patches of grasses and shrubs. This interpretation is consistent with the few other data sets available regarding historic environments in northern Patagonia. Both pollen records and beetle assemblages from this region suggest that the LGM was characterized by persistent low temperatures, strong winds, and prolonged snow cover. For areas east of the Andes, the only evidence of habitat conditions during this period comes from palynological data collected at Mallín Aguado (~25 km SW of ACoI; Markgraf and Bianchi, 1999). This record, which dates to ca. 17,000 yr, suggests that the predominant habitat was steppe-like, consisting of largely

treeless expanses of grasses and shrubs (Markgraf et al., 2002). West of the Andes, pollen records from Fundo Llanquihue and Alerce (~150 km W of ACoI) suggest that ca. 20,000 yr, the Chilean Lake District was characterized by high Andean steppe consisting of a mix of grasses and shrubs punctuated by bog-like areas and small patches of Subantarctic forest (Heusser, 2003; Heusser et al., 2006); consistent with this, the average summer temperature at the time is estimated to have been 6–7°C cooler than today (Moreno, 1997). A similar landscape is suggested by the fossil fauna of cold-adapted beetles documented from this region (Hoganson and Ashworth, 1992; Ashworth, 2006). Thus, in general, LGM habitats from northern Patagonia appear to have been more open, barren, and colder than the habitats in the region today.

The LGM fauna from ACoI also yields insights into local patterns of glaciation. Several lines of evidence suggest that glaciers continued to cover large portions of the eastern slope of the Patagonian Andes at ca. 15–14 ka (McCulloch et al., 2000; Glasser et al., 2004). After the LGM, as the glaciers retreated, the landscape in northern Patagonia is thought to have been dominated by large lakes (Tatur et al., 2002). Along the Andean precordillera, extensive bodies of water formed when terminal moraines dammed existing drainages. This is thought to have coincided with a pluvial phase that peaked about 16.5 ka, as estimated from dates obtained from carbonates collected near Maquinchao (cf. Tatur et al., 2002), ca. 200 km east of the Limay Valley. As a result, lakes rose to the highest levels known for both the Patagonian steppe (e.g., Galloway et al., 1988; Cartwright et al., 2011) and central, semiarid Argentina (Bebadero basin; Gonzales et al., 1981). The changes in composition of the small mammal assemblages examined here – in particular, the increased mammalian diversity evident beginning in the early Holocene – are consistent with this general climatic change.

Finally, the faunal record revealed by owl pellets from ACoI can be used to infer the location of forest habitat during the LGM. Rodent species that today typically occur in forest or shrub–forest habitats (e.g., *Geoxus*, *Irenomys*, *Loxodontomys*, *Oligoryzomys*) are rare or missing from the earliest levels examined at ACoI, suggesting that the surrounding area was not forested during this period. Although this could be attributed to the tendency of Barn Owls to hunt in open habitats, analyses of pellets deposited by *T. alba* nesting in or near forested areas revealed that those animals preyed heavily on forest-dwelling rodents (Trejo and Ojeda, 2004; Udrizar Sauthier et al., 2005). This suggests that if a patch of forest habitat had been located near ACoI during the LGM, we would have detected the presence of forest-dwelling rodents in the samples excavated from the cave.

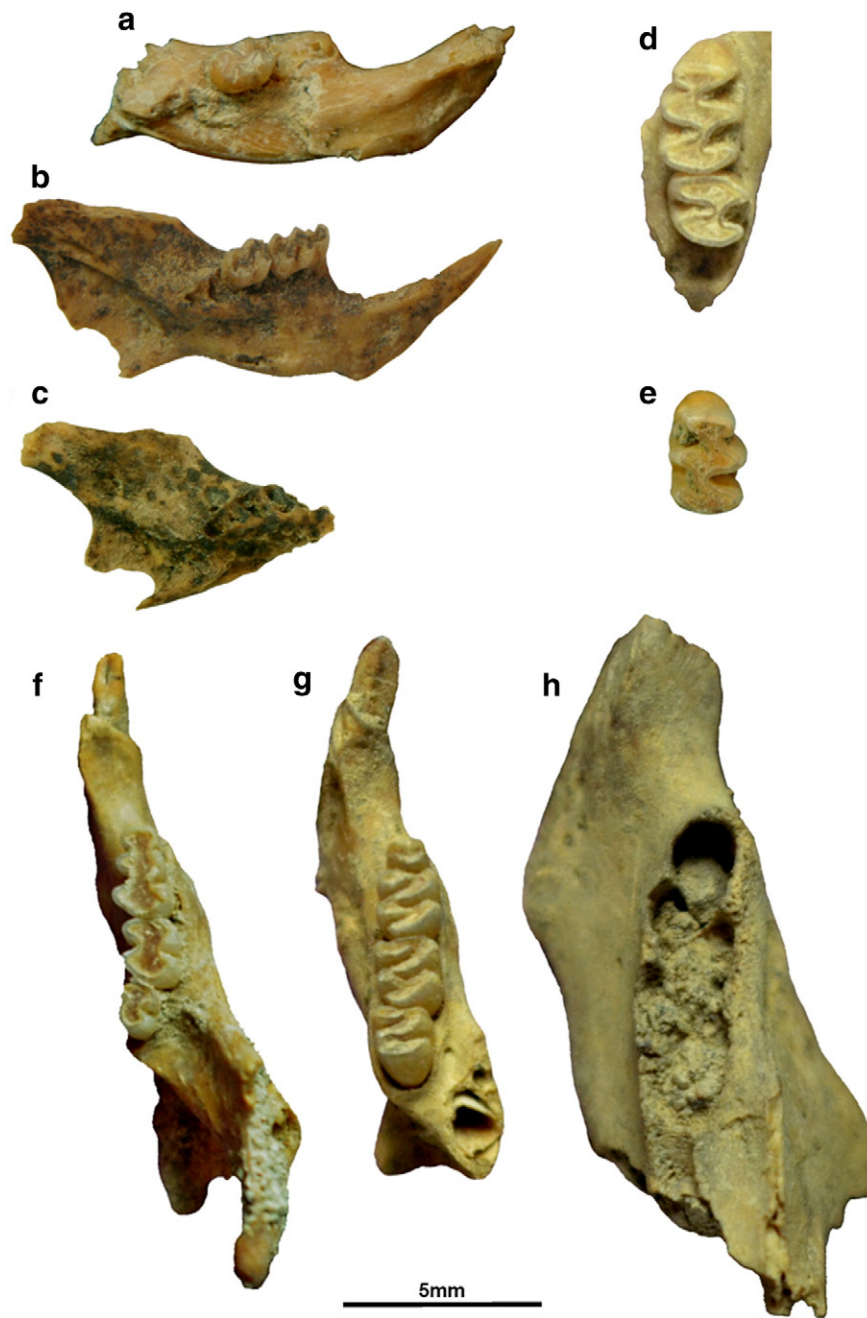


Figure 4. Representative examples of small mammal specimens obtained from ACol levels V–VII, which correspond to the LGM. Shown are the left mandibles (labial views) of (a) *Abrothrix longipilis* [with m3], (b) *A. olivaceus* [with m2–3] and (c) *Eligmodontia morgani* [with alveoli]. Also shown are the left maxillae of (d) *Phyllotis xanthopygus* [with M1–3] and an isolated right M1 molar of (e) *Loxodontomys micropus*. Finally, right mandibles (occlusal views) are shown for (f) *Chelemys macronix* [with m1–3], (g) *Euneomys chinilloides* [with m1–3] and (h) *Ctenomys sociabilis* [with alveoli].

The location of the LGM terminal moraine indicates that the edge of the ice shield was about 10 km SW of ACol, near the mouth of the Limay River. The hilly terrain (elevation >1500 m) immediately to the west of the cave, suggests that ACol was not covered by ice but was characterized by cold and dry conditions, making the presence of a forest refugium in this area unlikely. This interpretation is supported by pollen records from Mallín Aguado; prior to 17,000 cal yr BP, this location was dominated by treeless steppe vegetation (Markgraf et al., 2002). Additionally, phylogeographic studies of several forest-dwelling small mammal taxa (e.g., *Dromiciops gliroides*: Amico and Aizen, 2000; Himes et al., 2008) as well as several plant taxa associated with Patagonian forests (e.g., *Nothofagus pumillo*; Mathiasen and Premoli, 2010) suggest that forested refuge areas were located in north-central Chile

and southern Mendoza Province in Argentina (Smith et al., 2001; Palma et al., 2012) as well as in the eastern Andes well to the south of ACol (latitudes >43°S; Premoli et al., 2000; Pastorino et al., 2009). Thus, the area surrounding ACol does not appear to have been forested during the LGM, adding further support to the hypothesis that the predominant habitat at this location was open grassland or shrub-land.

Changes in the mammalian fauna

Given the apparent similarity between the inferred LGM habitat at ACol and current high Andean habitats, it is perhaps not surprising that the small mammal assemblages recovered from ACol are somewhat depauperate. Modern small mammal communities from presumably

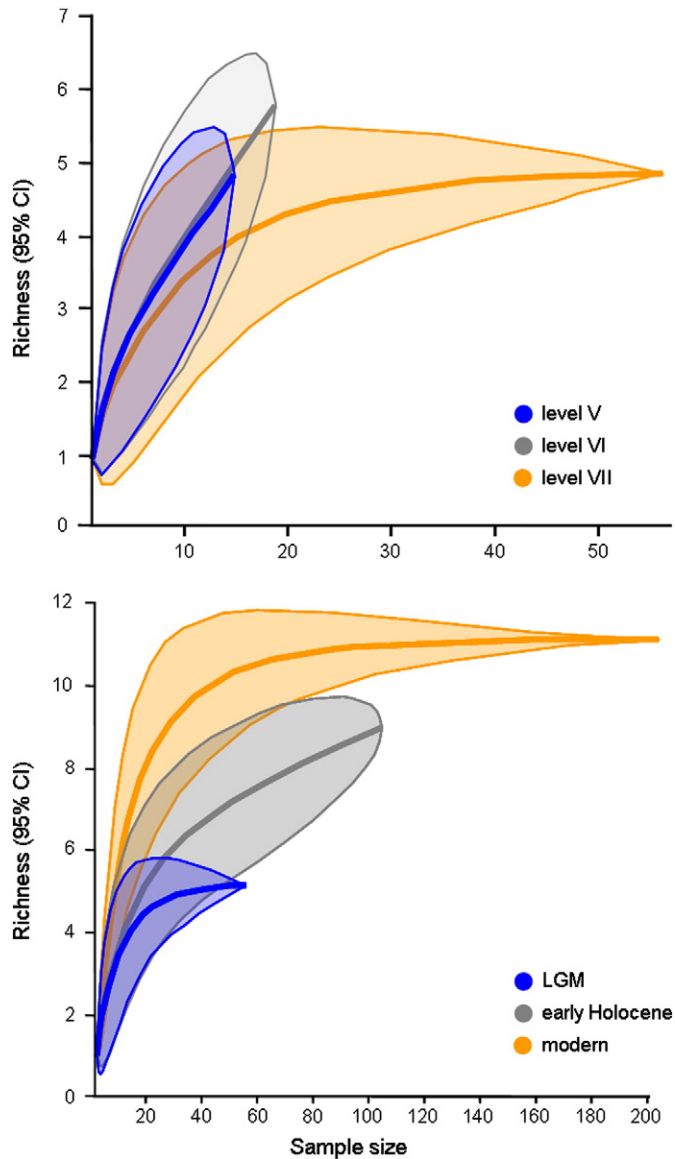


Figure 5. Rarefaction analyses for fossil LGM assemblages from ACol (upper panel), and for across time periods (bottom panel) include early Holocene (10 ka) and modern samples from ACol, and LGM samples from ACol (all levels pooled). For all samples, 95% confidence intervals are shown.

similar high elevation Andean habitats contain relatively limited taxonomic diversity, typically consisting of a few members of the Abrotrichini and Phyllotini as well as *Euneomys* (Reise and Venegas, 1987; Pearson, 1995; Pardiñas et al., 2003). In contrast, the ecotone habitat present at ACol today – a mosaic of grassland, open shrubland, and small patches of forest – is typically associated with greater species diversity (Pearson and Pearson, 1982). Thus, the increase in species richness and diversity over time evident in our samples is consistent with changes from the inferred LGM environment to the modern habitats in the Limay region. Overall, this suggests that most responses to changing climatic conditions occurred in situ (see Terry et al., 2011), with a major faunal shift resulting from the immigration of new taxa associated with forested habitats ca. 9–10 ka.

Temporal changes in the prevalence of two species are particularly noteworthy. First, our data revealed a pronounced decline in the relative abundance of *E. chinchilloides* since the LGM. In montane areas near Aconcagua (elevation 2850 m) in northwestern Argentina, this species represents >50% of the prey consumed by owls (Pardiñas et al., 2010), suggesting that these animals represent an important food resource for

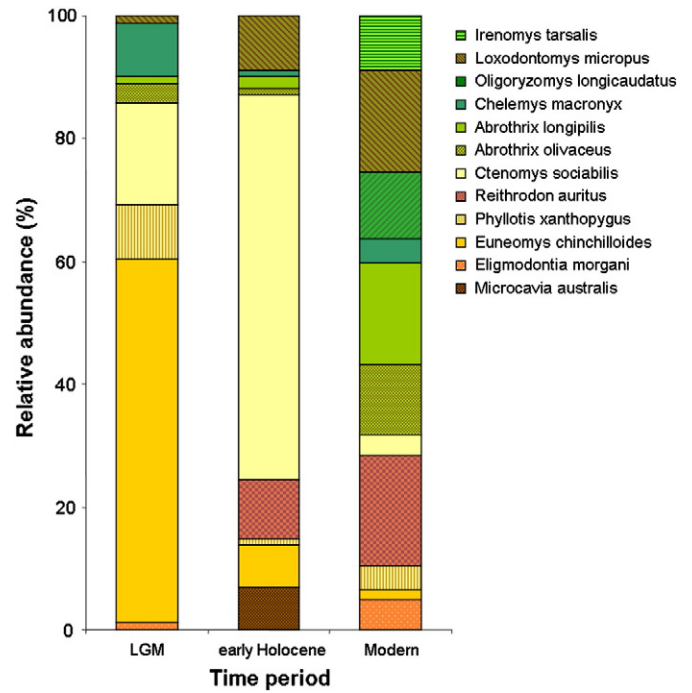


Figure 6. Temporal changes in the relative abundance of small mammal species in the Limay Valley region. Data shown are from the LGM (ACol), the early Holocene (AColl), and modern owl pellets (AColl). Estimates of relative abundance were calculated from analyses of MNI values for each species.

at least one avian predator in this ecosystem. At ACol, *E. chinchilloides* went from being the most abundant small mammal species (~60% of material identified) during the LGM to being one of the least common (<5% of material identified) in modern samples from this locality (see also Pearson, 1987; Rebane, 2002; Pardiñas and Teta, 2013). In addition to the implications of this finding for inferences regarding historic and modern environments (see above), this dramatic shift in the composition of the small mammal fauna of ACol seems likely to have had important consequences for other elements of the local biota, such as the predators in this region that relied on *E. chinchilloides* as a food resource.

A marked decrease in the abundance of *C. sociabilis* since the LGM was also detected. This species is endemic to the Limay region (Pearson, 1995), where it is associated with mesic patches of grass and shrub land (Tammone et al., 2012). Comparisons of historic samples from Cueva Traful and modern populations of this species suggest that it has undergone a significant loss of genetic variability over the last 3000–5000 years (Chan et al., 2005). One proposed explanation for this reduction in genetic variability is loss of suitable habitat due to changes in environmental conditions. The open grassland and shrubland habitat thought to have occurred in this region immediately after the last major glacial retreat (Markgraf et al., 2002) would have favored *C. sociabilis*. As *Nothofagus* forest and cypress began to increase in prevalence in the early Holocene, however, much of this open habitat may have disappeared, leading to the decrease in relative abundance and genetic diversity reported for *C. sociabilis* (Chan et al., 2005).

In sum, our analyses of fossil mammal assemblages obtained from owl pellets collected at ACol have generated important new insights into the environment present at this locality during the LGM. Our analyses suggest that during this period, the Limay Valley region of Patagonia was characterized by open, barren, cold habitats of the type found today at high elevation locations in the Andes mountains. Associated with habitat changes at this locality over the past ca. 20,000 years are pronounced changes in the small mammal community, notably marked decreases in two previously predominant species, *E. chinchilloides* and *C. sociabilis*. In addition generating insights into the ecological histories of these two taxa, these analyses suggest important changes in the

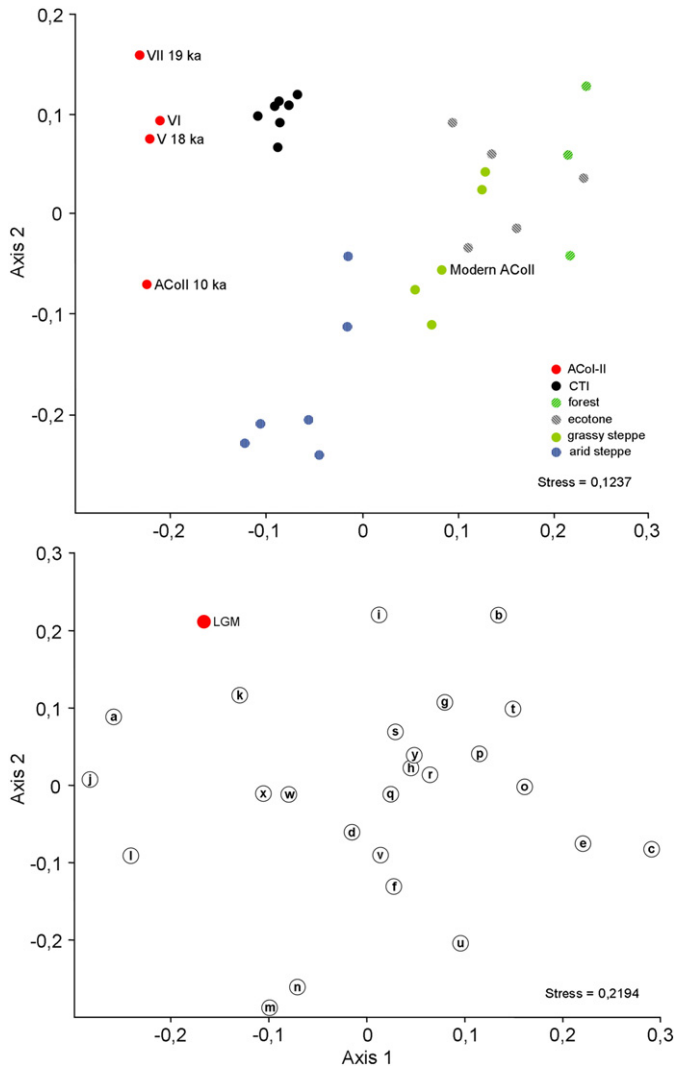


Figure 7. NMDS ordination plots for modern and fossil small mammal assemblages from Patagonia. Upper panel: analyses of samples from the Limay Valley region, including fossil assemblages from Corral's caves and CTI, and modern samples by habitat type from the 19 localities listed in Table 2. Bottom panel: analyses of samples from a larger area of Patagonia. Letters refer to the 25 modern sampling localities listed in Table 1. For both panels, the stress value indicates the concordance between the data matrix and the 2-dimensional plane; high stress values = 1 indicate a poor fit between these parameters.

larger communities in which these animals occurred. Future studies will focus on integrating these data with more detailed analyses of the historical demography and genetics of *E. chinchilloides* and *C. sociabilis* in order to better understand the ecological and evolutionary consequences of temporal changes in environmental conditions in Patagonia.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2014.04.015>.

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