



Combination of humans, climate, and vegetation change triggered Late Quaternary megafauna extinction in the Última Esperanza region, southern Patagonia, Chile

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South America lost around 52 genera of mammals during a worldwide event known as the Late Quaternary Extinction episode. More than 80% of South American mammals weighing > 44 kg succumbed. Analysis of the megafaunal extinction chronology in relation to human arrival and major climate changes have revealed slightly different extinction patterns in different eco-regions of the continent, highlighting the importance of detailed regional analysis in order to understand how the possible drivers of extinction operated. Here we present an analysis of the megafaunal extinction in the Última Esperanza (UE) area of southwestern Patagonia, Chile. We have compiled a comprehensive chronology of megafaunal extinctions and earliest human occupation between 18–7 cal ka BP, based on radiocarbon dates from published literature. We calculated confidence intervals using the GRIWM method to estimate the times of human arrival and megafaunal local extinctions, and then compared these events to the timing of major climate and vegetation changes, fire frequency increase, and the Reclús volcanic eruption. Our results suggest that a combination of human impacts and climate–vegetation change drove megafaunal extinctions in the UE area, with the balance of factors being taxon specific; the volcanic eruption does not seem to have exacerbated extinctions. Competition between humans and mega-carnivores seems to be the most plausible cause for the extinction of the mega-carnivores. Coexistence of humans with extinct horses, extinct camels, and mylodonts for several thousand years rules out a scenario of blitzkrieg overkill of megafauna by humans. The transition of vegetation from cold grasslands to *Nothofagus* forests corresponds with the disappearance of *Hippidion saldiasi* and *Lama cf. owenii*. The later full establishment of *Nothofagus* forests and an increasing fire frequency coincided with the disappearance of mylodonts. A climate-driven reduction of open environments plausibly reduced herbivore's populations making them susceptible to local extinction.

By the end of the Pleistocene, the world lost about half of its terrestrial megafaunal species (average body weight exceeding 44 kg) in an event known as the Late Quaternary Extinction episode (LQE) (Martin 1967, 1990, Martin and Klein 1984, Martin and Steadman 1999, Barnosky et al. 2004, Koch and Barnosky 2006). In sheer numbers, South America lost more genera (52) and species (~ 66) than any other continent (Brook and Barnosky 2012). As on other continents, the primary debates about the causal mechanism of the LQE in South America revolve around the relative importance of humans, environmental change, and interactions between the two (Martin and Steadman 1999, Cione et al. 2003, Barnosky and Lindsey 2010). Nevertheless, the resolution of these debates is difficult without detailed chronologies and sound mechanistic underpinnings. In South America, the general picture has suggested that the

chronology of extinction roughly coincided with major climatic changes that occurred during the Pleistocene–Holocene transition and also with the first arrival of humans into the South American continent (Koch and Barnosky 2006). However, recent work that synthesizes information from many investigators suggests somewhat different extinction chronologies in different eco-regions of the continent, that taken at face value suggest that extinction may have started in the north before human arrival and occurred later in higher latitudes, after humans were present and where climate changes were more severe (Barnosky and Lindsey 2010). The apparent differences in different regions emphasizes the need for highly resolved chronologies that compare the timing of megafaunal extinction, human arrival and population growth, and environmental change at the local and regional scale. Here, we attempt this for the Última

Esperanza area, south western Patagonia, Chile (Fig. 1), with the goal of better understanding the relative roles of humans versus environmental change as a driver of the extinction of several species of large mammals that disappeared from this region.

Located between 51°29'–51°40'S and 72°28'–72°43'W, the Última Esperanza region has been the focus of intense archaeological and paleontological research since the discovery of Cueva del Milodón (Myloodon Cave) in 1895 (Martinic 1996), research that also includes some of the earliest insights into the causes of the local megafaunal extinction (Borrero 1977). As a result, the region now offers what is one of the most comprehensive chronologies of megafaunal occupation for the South American continent, along with some of the earliest archaeological sites. In addition, a wealth of paleoenvironmental proxies have become available in the form of pollen data, charcoal records, isotopic studies, glacial data, and geomorphic and geological information. The sensitivity of these paleoenvironmental proxies is enhanced by Última Esperanza's location at the southern edge of the Southern

Westerly Winds (SWW), a climatic boundary that can produce marked regional and zonal effects as it shifts slightly north and south in response to global forcings.

These data revealed a relatively detailed history of the Última Esperanza area from the Last Glacial Maximum (LGM) to the Holocene. In general terms, the area changed from a completely glaciated landscape to one dominated by cold grasslands that were rapidly colonized by a dozen megafaunal taxa and by humans as the LGM gave way to the Holocene (see sections 4, 6, and 8). A massive volcanic eruption from the Reclús Volcano (50°57'S, 73°35'W) also occurred near the LGM–Holocene transition (see section 5). By the early Holocene most of the megafaunal taxa had disappeared, humans persisted, the landscape became dominated by *Nothofagus* forests, and fire frequency increased (see sections 6, 7, 9, and 10). In this study we examined in detail the timing of these dramatic changes in order to cast light on the most important drivers of megafaunal disappearance in the Última Esperanza region. We present a comprehensive compilation of radiocarbon dates on extinct fauna and on early human occupation in the region, all of them vetted from published literature, and used statistical techniques to place likely temporal bounds on the earliest occurrence of humans and latest occurrence of other megafauna. We then compared the arrival and extinction chronologies to the timing of major climate changes, vegetation changes, fire frequency, and volcanic activity gleaned from highly resolved paleoenvironmental proxies. Finally, we used this integrated information, along with inferences about the biology of affected megafaunal species, to draw conclusions about the relative roles of humans versus environmental perturbations in triggering the local collapse of the megafauna in Última Esperanza.

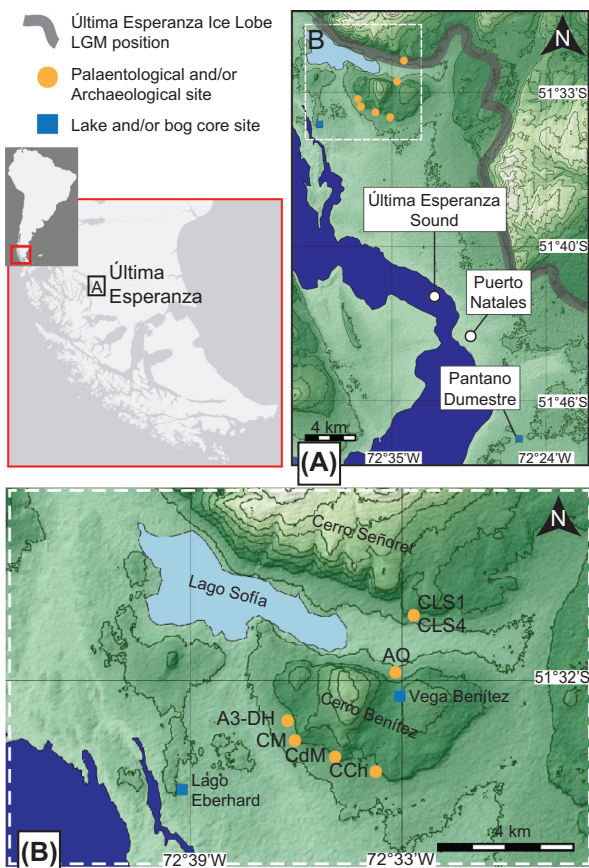


Figure 1. Study area. (A) General view of the Última Esperanza area. The location of the bog and lake records discussed in the text (blue rectangles) and the Last Glacial Maximum (LGM) extension of the Última Esperanza Ice Lobe estimated by Sagredo et al. 2011 (dark transparent thick line) are shown. (B) Closer view of the Cerro Benítez, Cerro Señoret, and Lago Sofía area. The distribution of the sites discussed in the text is shown. Abbreviations are: CLS1 = Cueva Lago Sofía 1; CLS4 = Cueva Lago Sofía 4; AQ = Alero Quemado; A3-DH = Alero 3 Dos Herraduras; CM = Cueva del Milodón; CdM = Cueva del Medio; CCh = Cueva Chica.

1. Study area

Our study area is located ~ 20 km north of Puerto Natales, with the paleontological, archaeological, and paleoenvironmental proxy localities distributed on and near the slopes of Cerro Benítez (~ 520 m a.s.l.) and Cerro Señoret (~ 372 m a.s.l.) (Fig. 1). Both of these high hills are located in the lee side of the Andes, 10 km inland from the east coast of the Última Esperanza sound (Fig. 1A and B). A glacial valley running east-west separates Cerro Benítez and Cerro Señoret and is today partially occupied by Lago Sofía. Most of the sites lie topographically above a late Pleistocene lake terrace developed on the flanks of Cerro Benítez and Cerro Señoret (see section 4). The paleontological and archaeological material typically comes from caves and rock shelters (see Table 1 for complete list and descriptions of localities, most of which are wave-cut excavations in the bedrock that resulted from erosion along the shores of the pro-glacial lake that existed at the time (Sagredo et al. 2011, Stern et al. 2011)).

2. Modern climate, vegetation and fauna

The climate of Patagonia is largely controlled by the Southern Westerly Winds (SWW), which deliver abundant precipitation derived from the Southeast Pacific Ocean. The

Table 1. Description of the sites discussed in this study. *Late Holocene archaeological radiocarbon dates have been reported for the site.

Site name	Geographic coordinates	Altitude (m a.s.l.)	General description and size	Interpretation	Taxon radiocarbon dates	Archaeological radiocarbon dates
Cueva del Milodón	51°33'54"S, 72°37'13"W	150	Large cave: ~ 250 m long, ~ 140 m wide, 30 m high in the entrance and 10 m high close to the back of the cave (Hauthal 1899, Borrero and Martin 2012).	Mainly paleontological. Middle to Early Holocene archaeological deposits have been described (Nordenskjöld 1900, Saxon 1976). Evidence of <i>Hippidion saldiasi</i> exploitation by humans has been found (Martin 2010, Prevosti and Martin 2013).	<i>Smilodon</i> : 2 <i>Mylodon</i> : 23 <i>M. darwini</i> : 1 Mylodontidae: 5 <i>Lama guanicoe</i> : 1	Charcoal: 4
Cueva del Medio	51°34'09"S, 72°36'12"W	150	Cave, 90 m long, 40 m wide and 6 m high (Nami 1985–1986).	Archaeological site. It has a late-Pleistocene human occupation with evidence of extinct fauna and modern fauna utilization. There are faunal remains with evidence of carnivore consumption (Nami and Menegaz 1991, Nami and Nakamura 1995).	<i>H. saldiasi</i> : 2 <i>L. cf. L. owenii</i> : 4 <i>L. guanicoe</i> : 3 <i>Mylodon</i> : 1 Mylodontidae: 2	Charcoal: 7, non-human bone: 12
Cueva Chica	51°34'23"S, 72°35'10"W	160–165	Consist of a main chamber and two inner dark chambers. In general, is about 70 m long and 17 m wide (Martin et al. 2013).	Paleontological site, carnivore den (Martin et al. 2013).	<i>L. gracilis</i> : 1 <i>P. onca mesembrina</i> : 1 <i>Panthera</i> : 2 Mylodontidae: 3 Mylodontidae: 2	None
Alero 3 – Dos Herraduras	51°33'35"S, 72°37'25"W	150	One of three exposed rockshelters under the name of Dos Herraduras. The R1 tephra is present (Borrero and Massone 1994).	Mainly archaeological. <i>Mylodon</i> has been found but association with archaeological evidences has been discarded (Borrero and Massone 1994).	None	None*
Alero Quemado	51°54'79"S, 72°57'64"W	150	Rockshelter. Eight meters long, 3 m wide, 3 m high-R1 tephra is present (Sierpe et al. 2009).	Mid-Holocene archaeological site. Incur-sion of terrestrial hunter gatherers to the coast. It has evidence of use of modern faunas (Sierpe et al. 2009).	None	Charcoal: 1
Cueva Lago Sofía 1	51°31'54"S, 72°34'12"W	150	30 m long, 8 m wide and 5 m high. It has evidence of ashes in its deposits (Prieto 1991).	Lower level is paleontological. Late Pleistocene occupation in upper levels (Prieto 1991, Massone and Prieto 2004, Jackson and Prieto 2005, Steele and Politis 2009).	<i>H. saldiasi</i> : 2 <i>L. guanicoe</i> : 1 <i>M. darwini</i> : 3	Charcoal: 1, bone: 4
Cueva Lago Sofía 4	51°31'54"S, 72°34'12"W	150	Dark chamber, 6 m long, 2.5 m wide and 1.5 m high (Prieto 1991).	Carnivore den (Prieto 1991, Borrero et al. 1997).	<i>Mylodon</i> : 1 <i>V. vicugna</i> : 3 Mylodontidae: 2	None

Andes cordillera presents a significant barrier to the low level wind circulation, with an orographic or 'rain shadow' effect that results in high precipitation on the western side of the Andes, and dry conditions on the east, in Argentine Patagonia (Carrasco et al. 2002, Garreaud et al. 2013). The amount of precipitation generally increases with altitude on the western side of the mountains and decreases down the lee eastern side. Annual precipitation at sea level can be as high as $\sim 4400 \text{ mm yr}^{-1}$ (Faro Evangelista $52^{\circ}24'S$, $75^{\circ}06'W$), and increases to $\sim 10\,000 \text{ mm yr}^{-1}$ in higher parts of the western Andes (Paso Galería $52^{\circ}45'S$, $73^{\circ}01'W$, 383 m a.s.l.), decreasing to $\sim 505 \text{ mm yr}^{-1}$ on the lee side (Punta Arenas, $53^{\circ}08'S$, $70^{\circ}53'W$, 6 m a.s.l.) (measurements taken between 1999 and 2002, Schneider et al. 2003). The Última Esperanza area is located between the hyper-humid climate of the western side of the Andes and the drier, more continental climates of the Argentine steppe. The closest meteorological measurements have been recorded in Puerto Natales ($51^{\circ}44'S$, $72^{\circ}31'W$, 2 m a.s.l., Fig. 1A), with mean annual precipitation values of 513 mm. Precipitation is fairly evenly distributed through the whole year, with slight maxima in March, April, August, and November. The mean annual temperature at the same station is between 6° and 7°C with an annual range of 9° – 10°C (Dirección Meteorológica de Chile < www.meteochile.gob.cl/inicio.php >).

The general climate patterns described above result in different vegetation communities as one proceeds from west to east across southern Patagonia: the Magellanic moorland, Magellanic evergreen forest, Magellanic deciduous forest, and the Patagonian steppe. The steep precipitation gradient produces forests primarily on the west side of the Andes, but lack of moisture limits penetration of forests eastward and results in a distinct forest-steppe ecotone that is characteristic on the east side of the Andes (Villa-Martínez and Moreno 2007, Moreno et al. 2009a). On the west side, the forests change with increasing altitude: the Magellanic evergreen forest gives way to deciduous forests at mid elevations, which are better able to resist low temperatures and prolonged snow cover (Lara et al. 2001). Above tree line the Andean desert dominates, which consists of a sparsely vegetated subnival alpine community.

Only three megafaunal species (mammals $> 44 \text{ kg}$) can be found in the region today: the guanaco *Lama guanicoe* (Camelidae), the south andean deer or huemul *Hippocamelus bisulcus* (Cervidae), and the puma *Puma concolor* (Felidae). Other common mammal taxa are the foxes *Pseudalopex culpaeus* and *Pseudalopex griseus*, Humboldt's hog-nosed skunk *Conepatus humboldtii* (Mustelidae), and a variety of rodents mainly from the families Muridae, Caviidae, Chinchillidae, and Ctenomyidae. Historical introductions of Leporidae include *Oryctolagus cuniculus* (European rabbit) and *Lepus capensis* (Cape hare), both of which are now broadly distributed and commonly found in the area. Among the most common large herbivores there is the ñandu, *Rhea pennata* (Aves) which weighs $\sim 25 \text{ kg}$.

3. Late Pleistocene–Holocene climate

Kilian and Lamy (2012) summarized key features of the climate change chronology in southern Patagonia, and

we review the salient information here. Land surface temperature estimations inferred from the EPICA Dome C (EDC) from east Antarctica show that by the LGM, between 20–18 ka BP, 100-yr mean surface temperatures over Antarctica were $\sim 10.3^{\circ}\text{C}$ colder than the mean of the last millennium. (Note that 'ka' indicates dates surmised from counting ice accumulation layers, and 'cal ka' indicates radiocarbon dates that have been calibrated to calendar years.) A warming event of $\sim 6.5^{\circ}\text{C}$ is recorded between 18–14.5 ka BP, which was followed by the Antarctic Cold Reversal (ACR), a rapid cooling event that dropped the 100-yr mean temperature $\sim 2^{\circ}\text{C}$ between 14.5–13 ka BP. The ACR was initially characterized by a rapid decrease in temperatures of $\sim 1.5^{\circ}\text{C}$ that took place over the first $\sim 500 \text{ yr}$ of its onset. After 13 ka BP, warming once again commenced, with 100-yr mean temperature eventually rising $\sim 4^{\circ}\text{C}$ by $\sim 11.9 \text{ ka BP}$ (Jouzel et al. 2007). This post-ACR warming is contemporaneous with the Younger Dryas cooling recognized in the northern hemisphere. Coeval with the Antarctic record of surface temperature, glaciers began to retreat in southwestern Patagonia during the first warming event recorded in the EDC. South of the Última Esperanza area, major ice lobes located over the Strait of Magellan ($53^{\circ}04'S$, $70^{\circ}38'W$) and Skyring sound ($52^{\circ}37'S$, $71^{\circ}50'W$) were already receding from their LGM maximum advance by $\sim 17.3 \text{ cal ka BP}$ and $\sim 18 \text{ cal ka BP}$ respectively (McCulloch and Davis 2001, Kilian et al. 2007). Near our study sites, the retreat of the Última Esperanza ice lobe started at $\sim 17.5 \text{ cal ka BP}$ (Sagredo et al. 2011; see section 4 for more details).

Warming beginning ca 18 ka BP seems characteristic of most of the southern part of the South American continent, the southern Pacific Ocean, and Antarctica, as indicated by concordance of several paleoclimate records, although the signal for the ACR is somewhat variable. Sediment analyses on the MD07/3128 marine core retrieved offshore of the Strait of Magellan ($52^{\circ}40'S$, $75^{\circ}34'W$) shows a warming over the Pacific Ocean at about the same time as the first warming event indicated in the EDC ice core, but starting slightly earlier, between 18–19 cal ka BP, and followed by a plateau of relatively stable temperatures coincident in time with the ACR (Caniupán et al. 2011). This same pattern is seen in the ODP1233 marine core extracted further north ($41^{\circ}00'S$, $74^{\circ}27'W$, Lamy et al. 2007). During the ACR, glacial readvances are reported in the Strait of Magellan ($53^{\circ}03'S$, $70^{\circ}37'W$) (Sugden et al. 2005), Torres del Paine ($50^{\circ}50'S$, $72^{\circ}49'W$) (Moreno et al. 2009b), and further north in the Lago Argentino area ($50^{\circ}35'S$, $72^{\circ}55'W$) located in the lee side of the Andes (Ackert et al. 2008, Kaplan et al. 2011, Strelin et al. 2014). Also coincident with the ACR, glaciers re-advanced in a proglacial lake environment in the Última Esperanza area between 14.8 and 12.8 cal ka BP (Sagredo et al. 2011).

Lake and bog cores from Lago Eberhard and Pantano Dumestre, both sites located close to the Última Esperanza area, provide records of vegetation and climate changes in the region during the Late Pleistocene–Holocene transition (Cárdenas 2006, Moreno et al. 2012). Positive water balance associated with stronger Southern Westerly Winds occurred between 14.6 and 11.8 cal ka BP, and especially between 13.6–12.6 cal ka BP, at Pantano Dumestre as is inferred from the low percentage of organic matter accumulation

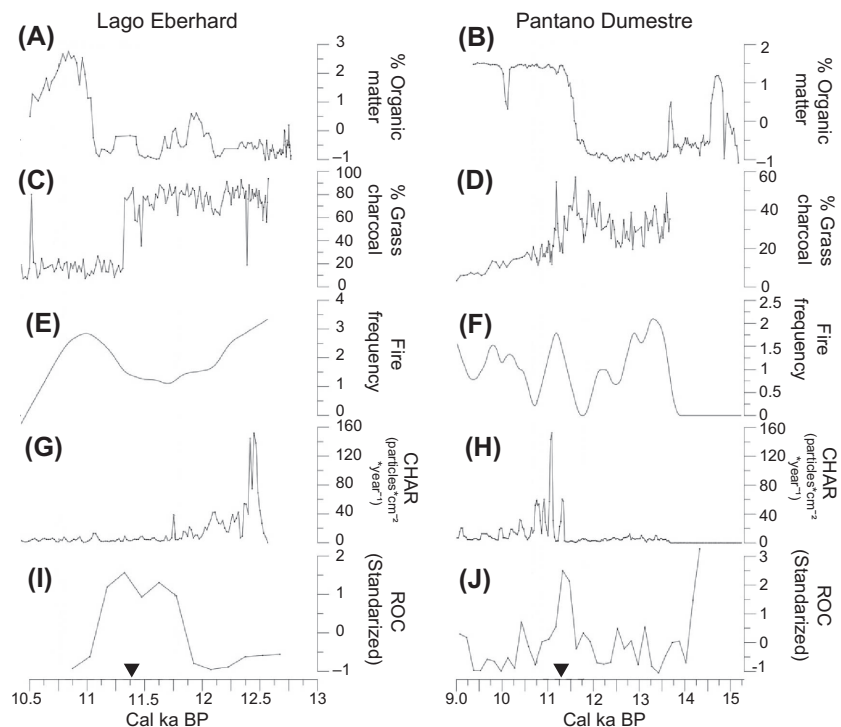


Figure 2. Comparison of the records of Lago Eberhard and Pantano Dumestre. (A–B) % of organic matter through time, (C–D) % of grass charcoal, (E–F) fire frequency, measured as fire events/500 yr, (G–H) charcoal accumulation rates analyses (CHAR), (I–J) rates of change analyses (ROC) in the pollen records. Information extracted and modified from Moreno et al. 2012. Black triangles show the timing of the onset in the increase of *Nothofagus* for each site.

that is related to subaqueous deposition at the site (Fig. 2B). Between 14.6 and 11.8 cal ka BP the area was probably cooler than present as inferred by a dominance of cold-resistant herbs in the pollen record (see section 6). Beginning at ca 11.8 cal ka BP, negative water balance is inferred at these sites implying a decline in the influence of the SWW and a subsequent decline in precipitation in the area (Fig. 2A and B). In addition, the expansion of *Nothofagus* trees indicates an increase in temperature during this time.

4. Glacial history and Puerto Consuelo pro-glacial lake

During the LGM, Andean glaciers formed a continuous ice cover in western Patagonia (38°–55°S); south of 43°S, the ice sheet reached the Pacific Ocean to the west and formed outlet glaciers over the Patagonian plains to the east (Holling and Schilling 1981). In the Última Esperanza region, outlet glaciers from the Patagonian Ice Sheet coalesced and formed the Última Esperanza Ice Lobe (UEIL) (Quensel 1910, Caldenius 1932, Meglioli 1992, Sagredo et al. 2011). By the last glacial termination (T1), the northern end of this lobe covered much of our study area (Fig. 1A). As temperatures started to rise near ~ 18 ka BP, the UEIL thinned and began to recede. The minimum age for local ice free conditions, at least in the Cerro Benítez area, is estimated to be ~ 17.6 cal ka BP derived from the most basal organic layer of the Vega Benítez bog core (Fig. 1A) (Sagredo et al. 2011). However, a date of ~ 18 cal ka BP ($14\,870 \pm 70$ ^{14}C yr) obtained from a *Lama gracilis* bone found at Cueva Chica (165 m a.s.l.)

(Martin et al. 2013, Table 2), just south of Vega Benítez, may indicate slightly earlier ice-free conditions for the Cerro Benítez area, although there is considerable overlap in the probability distributions of the two dates.

As the UEIL retreated, the Puerto Consuelo pro-glacial lake developed in sectors at elevations below the spillways or meltwater channels associated with the LGM moraines (Sagredo et al. 2011). A series of erosional lake terraces, paleo-shoreline caves, and bog and lake deposits containing clay-rich pebbly muds are evidence for the presence of this lake (Stern et al. 2011). In the Cerro Benítez and Cerro Señoret area, a terrace is prominent at 150 m a.s.l., and above it are located wave-cut caves where most of the megafauna and human remains we discuss here were found. These caves would have been on an island when the lake level was at 150 m a.s.l. (Sagredo 2007); the water level had to drop at least below 120 m a.s.l. to connect the cave-bearing island fully to the mainland (Stern et al. 2011). A *Mylodon* bone found in Cueva del Milodón produced a date of ~ 16.4 cal ka BP, indicating that by that time the lake level must have been below 150 m a.s.l. A *Lama gracilis* bone from Cueva Chica (165 m a.s.l.) produced a somewhat earlier date, ~ 18 cal ka BP, suggesting either that some of the caves may have been connected to mainland by land bridges before the lake level dropped < 120 m a.s.l. and after the area was ice free, or that animals swam to the island. The presence of the R1 derived tephra (see section 5) in some of the caves at Cerro Benítez (Alero Quemado, Alero Dos Herraduras, and Cueva de la Ventana) suggests that by ~ 14.9 cal ka BP the lake level must have been lower than 150 m a.s.l. (Stern et al. 2011).

Table 2. Radiocarbon dates on megafauna (extinct and extant) from the Última Esperanza area of rank 11 or higher, which are considered robust according to the scale published in Barnosky and Lindsey 2010.

Site name	Taxa (family, genus or species)	Lab number	14C age (uncalibrated) * AMS	Material dated	Calib median	Calib old	Calib young	Rank	Reference
Cueva del Medio	<i>Hippidion saldiasi</i>	NUTA-1811	10710 ± 100*	bone	12605	12755	12403	12	Nami and Nakamura 1995
Cueva del Medio	<i>Hippidion saldiasi</i>	NUTA-2331	10860 ± 160*	bone	12733	13076	12418	12	Nami and Nakamura 1995
Cueva Lago Sofia 1	<i>Hippidion saldiasi</i>	OXA-9319	10780 ± 60*	bone	12684	12743	12627	12	Steele and Politis 2009
Cueva Lago Sofia 1	<i>Hippidion saldiasi</i>	OXA-9504	10310 ± 160*	bone	12005	12457	11392	12	Steele and Politis 2009
Cueva del Medio	<i>Lama cf. L. owenii</i>	NUTA-2197	11040 ± 250*	bone	12893	13430	12407	12	Nami and Nakamura 1995
Cueva del Medio	<i>Lama cf. L. owenii</i>	NUTA-1734	10430 ± 100*	bone	12233	12558	11929	12	Nami and Nakamura 1995
Cueva del Medio	<i>Lama cf. L. owenii</i>	NUTA-1737	11120 ± 130*	bone	12935	13155	12714	12	Nami and Nakamura 1995
Cueva del Medio	<i>Lama cf. L. owenii</i>	NUTA-2330	10960 ± 150*	bone	12833	13094	12632	12	Nami and Nakamura 1995
Cueva Chica	<i>Lama gracilis</i>	Beta-288231	14870 ± 70*	bone	18036	18263	17838	12	Martin et al. 2013
Cueva del Medio	<i>Lama guanicoe</i>	NUTA-1735	10450 ± 100*	bone	12257	12564	11947	12	Nami and Nakamura 1995
Cueva del Medio	<i>Lama guanicoe</i>	NUTA-2332	10710 ± 190*	bone	12542	12979	12000	12	Nami and Nakamura 1995
Cueva del Medio	<i>Lama guanicoe</i>	NUTA-1812	10850 ± 130*	bone	12723	13013	12541	12	Nami and Nakamura 1995
Cueva del Milodón	<i>Lama guanicoe</i>	BM-1207a	7785 ± 747	bone	8698	10512	7155	11	Saxon 1979
Cueva Lago Sofia 1	<i>Lama guanicoe</i>	OXA-8635	10710 ± 70*	bone	12629	12725	12542	12	Steele and Politis 2009
Cueva del Medio	<i>Mylodon</i>	NUTA-2341	12720 ± 300*	bone	14968	15937	13996	12	Nami and Nakamura 1995
Cueva del Milodón	<i>Mylodon</i>	A-1390	13560 ± 190	sloth dung	16294	16900	15754	11	Long and Martin 1974
Cueva del Milodón	<i>Mylodon</i>	R-4299	13500 ± 410	hair and skin	16202	17476	15005	11	Long and Martin 1974
Cueva del Milodón	<i>Mylodon</i>	A-1391	10400 ± 330	hide	12068	12863	11166	11	Long and Martin 1974
Cueva del Milodón	<i>Mylodon</i>	SA-49	10200 ± 400	dung	11790	12743	10652	11	Long and Martin 1974
Cueva del Milodón	<i>Mylodon</i>	GX-6248	10575 ± 400	dung	12242	13164	11189	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	GX-6243	10880 ± 300	dung	12707	13319	11920	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	GX-6246	11775 ± 480	dung	13699	15127	12705	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	GX-6247	11905 ± 335	dung	13785	14912	13064	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	GX-6244	12020 ± 460	dung	14020	15359	12912	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	A-2445	12270 ± 350	dung	14329	15386	13388	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	A-2447	12240 ± 150	dung	14142	14837	13730	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	GX-6245	12285 ± 480	dung	14398	15780	13182	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	A-2448	12870 ± 100	dung	15309	15701	14996	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	A-2446	13470 ± 180	dung	16162	16747	15633	11	Markgraf 1985
Cueva del Milodón	<i>Mylodon</i>	BM-1375	12552 ± 128	dung	14706	15170	14168	11	Saxon 1979
Cueva del Milodón	<i>Mylodon</i>	BM-728	12984 ± 76	bone	15471	15748	15211	11	Burleigh et al. 1977
Cueva del Milodón	<i>Mylodon</i>	C-484	10832 ± 400	dung	12586	13420	11587	11	Arnold and Libby 1951
Cueva del Milodón	<i>Mylodon</i>	W-2998	13040 ± 300	hide	15517	16368	14330	11	Martinić 1996
Cueva del Milodón	<i>Mylodon</i>	LP-49	10377 ± 481	bone	11982	13095	10661	11	Tonni et al. 2003
Cueva del Milodón	<i>Mylodon</i>	LP-34	10812 ± 325	dung	12598	13302	11692	11	Tonni et al. 2003
Cueva del Milodón	<i>Mylodon</i>	LP-255	11330 ± 140	dung	13147	13417	12826	11	Borrero et al. 1991
Cueva del Milodón	<i>Mylodon</i>	LP-257	12570 ± 160	dung	14729	15264	14123	11	Borrero et al. 1991
Cueva del Milodón	<i>Mylodon</i>	Beta-164896	13480 ± 40	bone	16168	16342	15978	11	Martin 2010
Cueva del Milodón	<i>Mylodon</i>	Beta-164895	13630 ± 50	bone	16370	16608	16171	11	Martin 2010

Continued

Table 2. (Continued).

Site name	Taxa (family, genus or species)	Lab number	14C age (uncalibrated) * AMS	Material dated	Calib median	Calib old	Calib young	Rank	Reference
Cueva Lago Sofía 4	<i>Myiodon</i>	PITT-0940	11590 ± 100	bone	13379	13570	13167	11	Borrero et al. 1997
Cueva Lago Sofía 1	<i>Myiodon darwini</i>	OXA-9506	12250 ± 110*	bone	14124	14647	13768	12	Steele and Politis 2009
Cueva Lago Sofía 1	<i>Myiodon darwini</i>	Gx-31641	9700 ± 100*	bone	10984	11236	10717	12	Borrero and Martin 2012 (P. Moreno pers. comm.)
Alero dos Herraduras	Myiodontidae	LP-421	11380 ± 150	bone	13193	13466	12853	11	Borrero and Massone 1994
Alero dos Herraduras	Myiodontidae	AA-12574	12825 ± 110	bone	15237	15651	14798	11	Martinic 1996, Borrero and Martin 2012
Cueva Chica	Myiodontidae	Beta-284437	13970 ± 70*	bone	16885	17152	16579	12	Martin et al. 2013
Cueva Chica	Myiodontidae	Beta-288230	14240 ± 60*	bone	17286	17507	17070	12	Martin et al. 2013
Cueva Chica	Myiodontidae	Beta-288227	10780 ± 50*	bone	12687	12739	12641	12	Martin et al. 2013
Cueva del Medio	Myiodontidae	AA-12577	11990 ± 100	bone	13791	14061	13555	11	Martinic 1996
Cueva del Medio	Myiodontidae	AA-12578	11570 ± 100	bone	13362	13556	13155	11	Martinic 1996
Cueva del Milodón	Myiodontidae	Lu-794	13260 ± 115	bone	15879	16236	15480	11	Håkansson 1976
Cueva del Milodón	Myiodontidae	BM-1208	13183 ± 202	bone	15749	16307	15159	11	Burleigh and Mathews 1982
Cueva del Milodón	Myiodontidae	BM-1209	12496 ± 148	dung	14608	15152	14084	11	Burleigh and Mathews 1982
Cueva del Milodón	Myiodontidae	BM-1210	11810 ± 229	dung	13620	14140	13121	11	Burleigh and Mathews 1982
Cueva del Milodón	Myiodontidae	BM-1210b	12308 ± 288	dung	14361	15255	13551	11	Burleigh and Mathews 1982
Cueva Lago Sofía 4	Myiodontidae	AA-11498	13400 ± 90	bone	16068	16325	15774	11	Borrero et al. 1997
Cueva Lago Sofía 4	Myiodontidae	NSRL-3341	11050 ± 60	bone	12874	13024	12730	11	Borrero 1999
Cueva Chica	<i>Panthera</i>	Beta-284439	12890 ± 60*	bone	15323	15590	15126	12	Martin et al. 2013
Cueva Chica	<i>Panthera</i>	Beta-319537	11470 ± 50*	bone	13266	13401	13137	12	Martin et al. 2013
Cueva Chica	<i>Panthera onca mesembrina</i>	Beta-288228	11520 ± 50*	bone	13328	13446	13200	12	Martin et al. 2013
Cueva del Medio	<i>Panthera onca mesembrina</i>	Ua-24687	11410 ± 80*	bone	13213	13380	13071	12	Martin 2008, Prevosti and Martin 2013
Cueva Lago Sofía 4	<i>Panthera onca mesembrina</i>	Gx-31643	10840 ± 60	bone	12711	12794	12652	11	Martin 2008, Prevosti and Martin 2013
Cueva del Milodón	<i>Smilodon</i>	OxA-14457	11420 ± 50*	bone	13217	13320	13093	12	Barnett et al. 2005
Cueva del Milodón	<i>Smilodon</i>	OxA-13717	11265 ± 45*	bone	13090	13192	12996	12	Barnett et al. 2005
Cueva del Medio	<i>Smilodon cf. S. populator</i>	Ua-37622	11100 ± 80*	bone	12918	13072	12745	12	Prieto et al. 2010
Cueva Lago Sofía 4	<i>Vicugna vicugna</i>	Ua-36261	13545 ± 100*	bone	16260	16603	15945	12	Labarca and Prieto 2009
Cueva Lago Sofía 4	<i>Vicugna vicugna</i>	Ua-33262	13200 ± 100*	bone	15796	16107	15401	12	Labarca and Prieto 2009
Cueva Lago Sofía 4	<i>Vicugna vicugna</i>	Uncertain	13100 ± 70*	bone	15642	15904	15329	12	Weinstock et al. 2009

The transition from glacio-lacustrine sedimentation to organic sedimentation seen in cores from Pantano Dumestre and Lago Eberhard between ~ 15.4–12.8 cal ka BP indicates that the lake level was between 70–80 m a.s.l. by that time. Prior to ~ 10.3 cal ka BP, the pro-glacial lake that had previously covered the Última Esperanza area was gone (Sagredo et al. 2011).

5. Reclús Volcano

The Reclús Volcano is located in the western side of the southern Patagonian Ice Field at ~ 50°57'S, 73°35'W (Harambour 1988), within 100 km to the north-west of Última Esperanza. The volcano erupted near the end of the Pleistocene (R1), sending out a tephra plume which produced distinctive ash deposits in several different environments in southwestern Patagonia. More than twenty radiocarbon dates on sediments below and above the tephra layer have dated the Reclús eruption at ~ 14.9 cal ka BP (12 685 ± 260 ¹⁴C yr) (Stern 2008, Stern et al. 2011). The eruption produced a volume of > 5 km³ of volcanic debris, (Stern et al. 2011) making it the largest eruption recorded during the Late Pleistocene-Holocene in the Austral Volcanic Zone (Stern 2008). Samples of R1 tephra can even be found in deposits located in Tierra del Fuego, more than 400 km south east of the Reclús Volcano location (Stern 2008).

A younger, thinner, and less spatially ubiquitous tephra from the Reclús volcano has been identified, which dates back to the early Holocene between 10.2–10.6 cal ka BP (AMS dates in Villa-Martínez and Moreno 2007).

6. Vegetation changes (Fig. 2I and J and Fig. 3)

Early attempts to reconstruct the late glacial vegetation of the Última Esperanza region relied primarily on the analyses of plant remains in *Mylodon* dung and sediments from Cueva del Milodón (Salmi 1955, Moore 1978, Markgraf 1985, Heusser et al. 1992). These studies suggested dominance of grasses and herbs reflecting the presence of grasslands or a cold tundra-like landscape during the deglaciation, changing to a shrub land during the early part of the Holocene and becoming dominated by evergreen *Nothofagus* forests during the early to middle Holocene.

More recently, detailed records of late Pleistocene through Holocene vegetation changes have been obtained from bog and lake cores in the region. Most relevant for this study are cores obtained from Pantano Dumestre and Lago Eberhard (Fig. 3).

Lago Eberhard (51°34'S, 72°40'W; 68 m a.s.l.; Fig. 1A) is the pollen site closest to Cerro Benítez, Lago Sofia, and Cerro Señoret. Lake and bog cores from this site record the vegetation and glaciolacustrine history of the area between ~ 12.8–10.4 cal ka BP. The pollen analyses reveal a dominance of cold-resistant herbs (Poaceae, *Acaena*, Asteraceae subfamily Asteroidea) between ~ 12.8 and 11.6 cal ka BP, deposited in a deep lake environment. Increase in *Nothofagus dombeyi* type pollen was prominent at ~ 11.2 cal ka BP, accompanied by an increase of the fern spore *Blechnum* (not shown in Fig. 3). Both taxa began their rise to high abundance by

~ 11.6 cal ka BP reaching a peak between ~ 11.1–10.8 cal ka BP. This maximum in *N. dombeyi* type pollen is accompanied by markedly increasing abundance of the *Nothofagus* parasite taxon *Misodendrum*, indicating the establishment of a closed-canopy *Nothofagus* forest with an understory of ferns. As discussed by Moreno et al. (2012), the establishment of *Nothofagus* at this time is probably related to an increase in temperature rather than to an increase in moisture since it occurred at a time of decreasing precipitation inferred from the apparent decrease in lake levels noted in the Pantano Dumestre sediment record. This is consistent with studies that identify temperature as exerting greater control on the distribution of *Nothofagus pumilio* in the Chilean Andes (Lara et al. 2005).

Thirty km to the south east of Lago Eberhard is Pantano Dumestre. The pollen analyses from cores recovered from this bog have revealed dominance of cold-resistant herbs (*Acaena*, Poaceae, Asteraceae subfamily Asteroidea, *Galium* type) between ~ 14.6 and ~ 11.5 cal ka BP, similar to what is seen at the beginning of the record from Lago Eberhard. This cold-resistant herb component is accompanied by small amounts of *Nothofagus dombeyi* type pollen at the beginning of the Pantano Dumestre record. Percentages of *Nothofagus dombeyi* type pollen start to increase, then oscillate near ~ 13.0 cal ka BP, followed by a marked decrease, then a more pronounced, sustained increase at ~ 11.4 cal ka BP. At this time there is also an increase in *Misodendrum* pollen, which marks the establishment of *Nothofagus* forests in the area. Poaceae pollen rapidly increases at the same time, peaking in abundance at ~ 11.6 cal ka BP and declining soon after that (Poaceae is not shown in Fig. 3). This increase in Poaceae has been interpreted as rapid colonization by grasses of the local area of Pantano Dumestre after the establishment of a more terrestrial bog environment and not as a regional signal for the establishment of grasslands in the area (Moreno et al. 2012).

In summary, both records – Pantano Dumestre and Lago Eberhard – suggest a landscape dominated by cold resistant herbs during the late glacial and the beginning of the Holocene (~ 12.8–11 cal ka for Lago Eberhard, ~ 14.6–11.5 cal ka for Pantano Dumestre), followed by a marked increase in *Nothofagus dombeyi* type (~ 12.2 for Lago Eberhard site and ~ 13 cal ka BP for Pantano Dumestre), culminating in the establishment of *Nothofagus* forests during the early Holocene (~ 11.1–10.8 cal ka BP for Lago Eberhard and ~ 11.4 cal ka BP for Pantano Dumestre). The offsets in timing of the changes among the two sites has been partially ascribed to edaphic factors, that is, the Lago Eberhard core is from a deep part of the lake and reflects a regional pollen signal, whereas the Pantano Dumestre record is from a bog site that reflects a more local signal. The overall rates of vegetation change (ROC) in the pollen records (Fig. 2I and J) are high between ~ 11.8–11.2 cal ka BP in Lago Eberhard and ~ 11.5 cal ka BP in Pantano Dumestre, coincident with the time intervals where the percentages of cold resistant herbs are dropping and the ones of *Nothofagus* are increasing, as the vegetation is changing from a cold grassland to a *Nothofagus* forest. This reflects the high rates of change of the vegetation in the landscape during these times.

At a regional scale (50°–54° S) vegetation changes inferred from pollen and bog records are consistent with the two

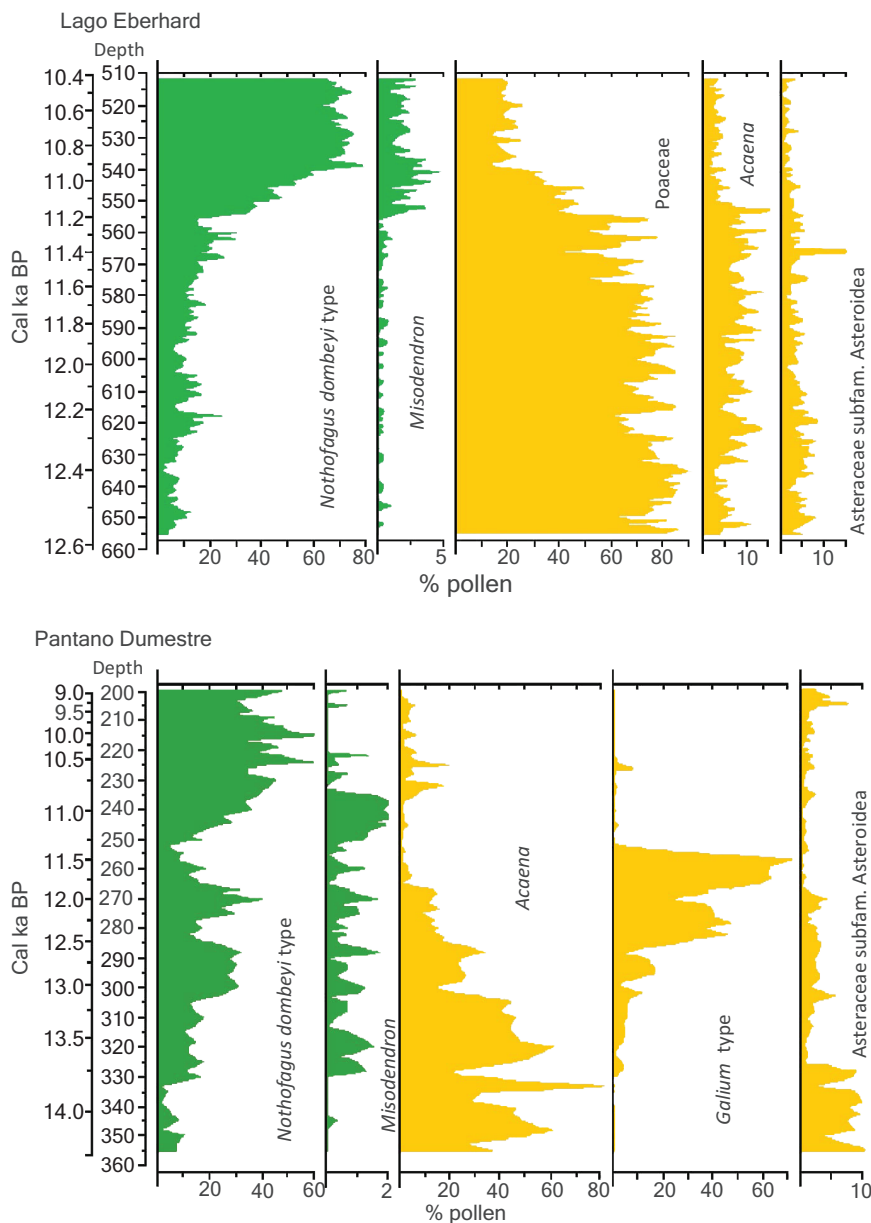


Figure 3. Percentage diagram of pollen from Lago Eberhard and Pantano Dumestre, modified from Moreno et al. 2012. Pollen percentages are shown as the proportion of terrestrial pollen total sum. Only taxa most informative for inferring vegetation changes relevant to megafauna extinction are shown. For a complete presentation and analysis of these records see Moreno et al. 2012.

described above in the sense that they show the presence of an open treeless landscape dominated by cold-resistant herbs and grasses during the deglaciation, followed by colonization by *Nothofagus* as temperature increases. Nevertheless, there are some differences in the vegetation structure evident from different areas, and more notably, in the details of timing of the vegetation changes. For example, sites located between (50°–53°S) show that the expansion of *Nothofagus* occurs ca 16 and 11 cal ka BP (Heusser 1995, Huber et al. 2004, Mancini et al. 2005, Villa-Martínez and Moreno 2007), while sites in the southern extreme of southern Patagonia (53°–54°S) show that the transition occurred much later and more abruptly between 11–9 cal ka BP (Markgraf 1993, McCulloch and Davies 2001, Huber et al. 2004, Ponce et al. 2011).

7. Fire history (Fig. 2C–H)

Macroscopic charcoal analyses from the cores retrieved at Lago Eberhard and Pantano Dumestre sites show a decline in the percentage of grass charcoal as *Nothofagus* became more persistent in the landscape (Fig. 2C and D). Both sites present high frequency of fire events at ~ 12.5 cal ka BP and between 11.6 and 10 cal ka BP (Fig. 2E and F), but events recorded at Lago Eberhard appear to be of greater magnitude at ~ 12.5 cal ka BP compared to the ones seen at Pantano Dumestre, with the reverse situation evident between 11.6 and 10 cal ka BP (Fig. 2G and H). In summary, both records coincide in showing a decline in fire frequency between ~ 12.7–11.6 cal ka BP, followed by an increase between 11.6–10.9 cal ka BP, which is coincident with a warm pulse, a decline in

precipitation and a general increase in *Nothofagus* forest cover. Finally there is a decline in fire frequency between ~ 10.9–10.5 cal ka BP (Moreno et al. 2012).

8. Late Pleistocene megafauna and humans (Fig. 4)

The late Pleistocene megafauna in Última Esperanza included the giant ground sloth *Mylodon darwini* (Mylodontidae), the American horse *Hippidion saldiasi* (Equidae), two species of extinct camels: *Lama gracilis* (Camelidae) and *Lama cf. owenii* (Camelidae), the saber tooth cat *Smilodon* (Felidae), the large jaguar *Panthera onca mesembrina* (Felidae), the bear *Arctotherium* (Ursidae), a member of the extinct mammal order Litopterna *Macrauchenia patachonica* (Macraucheniiidae), and the extinct fox *Dusicyon avus* (Canidae). Other taxa reported from Última Esperanza include the vicuña *Vicugna vicugna* (Camelidae), which is locally extinct and today survives only in the high central Andes, the extant guanaco *Lama guanicoe* (Camelidae), undetermined deer (Cervidae), and the culpeo fox *Pseudalopex culpaeus* (Canidae) (Nami and Menegaz 1991, Latorre 1998, Carrasco 2009, Martin 2010). The extant *Puma concolor* has not been described from Late Pleistocene deposits of Última Esperanza, but it has been documented at Cerro Sota (52°04'S, 70°03'W, east southern Patagonia) presumably from late Pleistocene deposits, (Miotti and Salemme 1999), although its age is questionable.

Remains of most of these taxa have been dated with a total of 67 robust published radiocarbon dates (Table 2) from the caves in and around Cerro Benítez and Cerro Señoret (Fig. 1), all of which are on bone, dung or skin from taxonomically identifiable elements. From the same vicinity are 25 published dates that record early human occupation (Table 3), all of which rank 11 or higher on the vetting scale published by Barnosky and Lindsey (2010). Of the archaeological dates, only 5 are of rank 13 or higher, which Barnosky and Lindsey (2010) considered the cut off for the most robust archaeological human occupation. We include archaeological dates of ranks 11 and 12 to increase sample size, which seems justified in this case in that they are consistent with the rank 13 dates.

All radiocarbon dates were calibrated using the Calib 7.01 program (Stuiver and Reimer 1986–2014) and the Southern Hemisphere calibration curve SH13 (Hogg et al. 2013). Most of the dates are for mylodont ground sloths, including 25 from specimens identified simply as *Mylodon* and three ascribed to *Mylodon darwini*. The extinct carnivores are represented by a total of 8 dates, of which 3 are on *Smilodon* (one of them cf. to *S. populator*) and 5 on *Panthera* (3 of them identified as *Panthera onca mesembrina*). *Hippidion saldiasi* and *Lama cf. L. owenii* are represented by 4 radiocarbon dates for each taxon. Finally, *Vicugna vicugna*, extirpated from the area but not extinct, is represented by 3 radiocarbon dates and *Lama gracilis* by a single date. For more details about the provenance of these dates see Table 1.

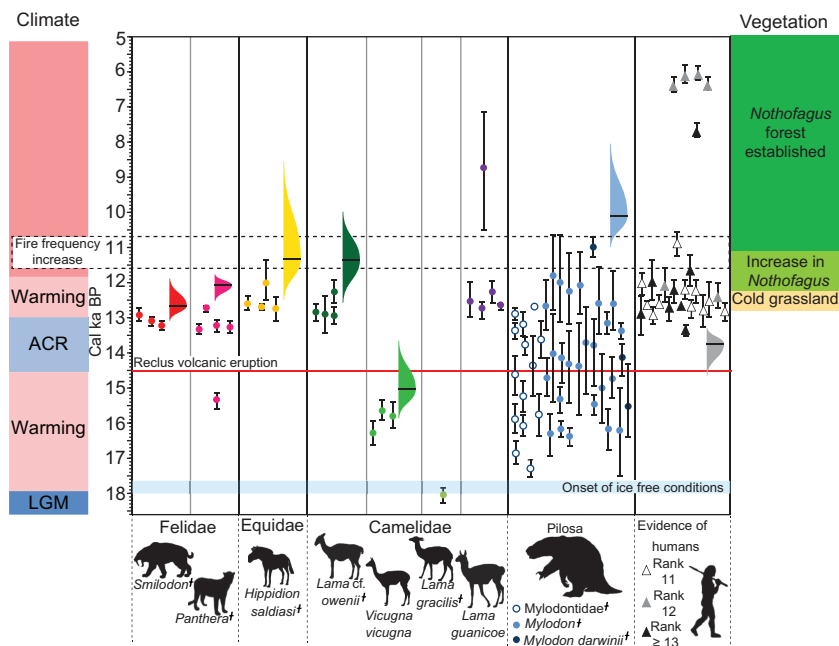


Figure 4. Chronology of megafaunal extinctions with estimated time of human arrival. Megafaunal extinction chronology is inferred from dates listed in Table 2 (colored dots) and the chronology of human arrival is based on dates from Table 3 (triangles, white, gray, and black indicate the different ranks calculated following Barnosky and Lindsey 2010). The GRIWM best-estimates of the time of extinction (or arrival in the case of the humans) is indicated by the colored normal distributions, with the 95% confidence band depicted by the colored areas around the mean (black line = most probable time of extinction). Warming and cooling events are inferred from the EDC Antarctic ice core (Jouzel et al. 2007, red and blue bands at left represent warming and cooling events respectively). Major vegetation changes (yellow, light green and dark green bands at right) and fire frequency information (black dashed rectangle) are extracted from Moreno et al. 2012. The timing of local ice free conditions estimated in Sagredo et al. 2011 (light blue dashed line rectangle) and the timing of the Reclus Volcano eruption (red line) is taken from Stern 2008 and Stern et al. 2011. The time axis is in calibrated years before present.

Table 3. Radiocarbon dates on evidence of human presence in the Última Esperanza area; all are ranked 11 or higher according to the scale in Barnosky and Lindsey 2010.

Site name	Lab number	14C age (uncalibrated) *AMS	Material dated	Archaeological evidence	Calib. median	Calib. old	Calib. young	Rank	Reference
Cueva del Medio	Beta 52522	10430 ± 80	charcoal	lithics, hearth	12233	12447	11965	11	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Medio	PITT 0344	9595 ± 115	charcoal	lithics, hearth	10893	11198	10574	11	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Medio	Gr-N 14913	10310 ± 70	charcoal	lithics, hearth	12010	12312	11756	11	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Medio	Beta 39081	10930 ± 230	charcoal	lithics, hearths	12795	13259	12370	11	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Medio	NUJA 1811	10710 ± 100*	bone	lithics, hearths	12605	12755	12403	11	Nami and Nakamura 1995
Cueva del Medio	NUJA 1737	11120 ± 130*	bone	lithics, hearths, burnt bone	12935	13155	12714	11	Nami and Nakamura 1995
Cueva del Medio	NUJA 2330	10960 ± 150*	bone	lithics, hearths, burnt bone	12833	13094	12632	11	Nami and Nakamura 1995
Cueva del Medio	NUJA 1735	10450 ± 100*	bone	lithics	12257	12564	11947	11	Nami and Nakamura 1995
Cueva del Medio	NUJA 2332	10710 ± 190*	bone	lithics	12542	12979	12000	11	Nami and Nakamura 1995
Cueva del Medio	NUJA 1812	10850 ± 130*	bone	lithics	12723	13013	12541	11	Nami and Nakamura 1995
Lago Sofía 1	OxA 8635	10710 ± 70*	bone	hearth, lithics	12629	12725	12542	11	Prieto 1991, Massone and Prieto 2004
Cueva del Medio	Beta 58105	10350 ± 130	burnt bone	fireplace, lithics	12100	12557	11602	12	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Medio	Gr-N 14911	10550 ± 120	burnt bone	fireplace, lithics	12409	12687	12026	12	Nami 1985–1986, Nami and Nakamura 1995
Cueva del Milodón	BM 1201a	5366 ± 55	charcoal	artifacts	6104	6219	5986	12	Saxon 1976
Cueva del Milodón	BM 1201b	5395 ± 58	charcoal	artifacts	6133	6283	5991	12	Saxon 1976
Cueva del Milodón	BM 1204b	5643 ± 60	charcoal	artifacts	6382	6506	6282	12	Saxon 1976
Cueva del Milodón	BM 1204a	5684 ± 52	charcoal	artifacts	6423	6551	6302	12	Saxon 1976
Cueva del Medio	NUJA 2331	10860 ± 160*	bone	fireplace, lithics	12733	13076	12418	13	Nami and Nakamura 1995
Cueva del Medio	NUJA 2197	11040 ± 250*	bone	fireplace, lithics	12893	13430	12407	13	Nami and Nakamura 1995
Cueva del Medio	NUJA 1734	10430 ± 100*	bone	fireplace, lithics	12233	12558	11929	13	Nami and Nakamura 1995
Lago Sofía 1	PITT 0684	11570 ± 60	charcoal	hearth	13367	13482	13238	13	Prieto 1991
Lago Sofía 1	OxA 9319	10780 ± 60*	bone	hearth, lithics	12684	12743	12627	13	Prieto 1991, Massone and Prieto 2004
Lago Sofía 1	OxA 9504	10310 ± 160*	bone	hearth, lithics	12005	12457	11392	13	Prieto 1991, Massone and Prieto 2004
Lago Sofía 1	OxA 9505	10140 ± 120*	bone	hearth, lithics	11670	12058	11245	13	Prieto 1991, Massone and Prieto 2004
Alero quemado	Ua 35652	6920 ± 50*	charcoal	lithics	7714	7834	7611	14	Sierpe et al. 2009

9. Estimating the last occurrences of the megafaunal taxa (Fig. 4)

With an incomplete fossil record the youngest fossil of a taxon typically predates the true time of its local extinction (Marshall 1990). A simple way of rectifying this bias is to extend the known temporal range a distance equivalent to the average temporal gap size between the fossils from within the known temporal range (Strauss and Sadler 1989). However, this method assumes that the likelihood of finding a fossil is the same everywhere within its true range – but if a taxon is being driven to local extinction by changing climate/vegetation and/or human activity, then the probability of finding fossils is likely to decrease as the taxon is going extinct. Furthermore, the likelihood of finding fossils may also vary through time due to a variety of changing taphonomic conditions. Finally, the uncertainties associated with the radiometric dates (Fig. 4) are often relatively large making it hard to determine the temporal gap sizes between the fossils. To accommodate these complexities we used the Gaussian-resampled, inverse-weighted method (GRIWM) of McNerny et al. described in Bradshaw et al. (2012) to estimate true times of local extinction. This approach deals with non-random fossilization by progressively up-weighting the gap sizes the closer they are to the time of disappearance from the fossil record. It also takes into account the uncertainties associated with the radiometric dates, providing a 95% confidence band around the estimated time of extinction. We also applied the method to estimate the true time of arrival of humans into the area. Analyses were run in the R programming environment (R Core Team) and the R code can be accessed in Saltré et al. 2015, appendix A – supplementary data.

Turning to the fossil record (Fig. 4), *Lama gracilis* disappears earliest, but this taxon is represented by only one date, so it is impossible to ascribe any significance to its time of disappearance (with only one fossil occurrence there are no gaps within its range, and thus no scale-length to judge how far beyond the last fossil the species became extinct). *Vicugna vicugna* also appears to drop out of the record early, with its time of local disappearance estimated to be between 13.7 and 15.9 cal ka BP. It is difficult to attribute much confidence to this, however, as this taxon is represented by only three dates. With fewer dates the GRIWM method tends to overestimate the uncertainty associated with the final extinction time (Bradshaw et al. 2012). A bootstrap technique discussed by Barnosky and Lindsey (2010), which mimics analytic methods (Marshall 1990, 2010), suggests that at least 10 dates are desirable for estimating true times of extinction.

As a guild, carnivores seem to disappear slightly earlier than any of the well-dated herbivores; this is the reverse of the general expectation that the demise of carnivores results from the loss of their megafauna prey, sometimes invoked to explain their extinction in the LQE event (for example, see the keystone hypothesis of Barnosky 1989, Owen-Smith 1989, Haynes 2002, Cione et al. 2003). The last appearance for *Smilodon* has a youngest limit of ~ 11.9 cal ka BP, with a best estimate: 12.6 cal ka BP, and for *Panthera*, an upper limit of ~ 11.7 cal ka BP, with a best estimate of 12.0 cal ka BP. In contrast, the best estimate for the disappearance of *Hippidion saldiasi* and *Lama owenii* is several hundred years

later, approximately 11.3 cal ka BP for both taxa, with upper limits at least 2000 yr later, but with oldest estimates (~ 12.6 cal ka BP) that might pre-date the time of disappearance of the large carnivores. Mylodont sloths drop out later yet, with the best estimate of their time of local extinction 10.1 cal ka BP, with an upper limit as young as 8 cal ka BP. There is no overlap between the probable extinction intervals of carnivores and mylodont sloths.

The GRIWM method estimates the earliest likely human arrival into the Última Esperanza area between 14.6 and 13.3 cal ka BP. Thus, it seems likely that humans began visiting the Última Esperanza region ~ 4000 yr after it became ice-free (Fig. 4), and well after *Panthera*, *Vicugna vicugna*, and *Mylodon* were well established in the region. Humans then locally co-existed with the extinct mylodonts, *Hippidion saldiasi* and *Lama cf. owenii* for several thousand years. The GRIWM confidence intervals suggest that *H. saldiasi* coexisted with humans for at least ~ 700 yr and could have coexisted for as long as ~ 5800 yr. *Lama cf. owenii* appears to have coexisted with humans for at least ~ 700 yr and perhaps as much as ~ 4700 yr. Mylodonts, probably co-occurred with humans for at least ~ 2300 years and perhaps for as much as ~ 6600 yr.

10. Causes of megafauna extinction (Fig. 4)

The pattern of extinction illustrated in Fig. 4 suggests that the timing of megafaunal extinction in the Última Esperanza region was controlled by a complex interaction between climate changes that precipitated vegetation change, combined with growing human impacts. Of particular note are: 1) the co-existence of megafauna with humans for at least hundreds and more likely thousands of years, although the archeological evidence suggests that human presence during this interval was probably ephemeral (Nami and Menegaz 1991, Jackson and Prieto 2005, Martin 2010; and further supported by the fact that Cueva del Milodón is less than 2 km away from Cueva del Medio – it seems unlikely that humans and mylodonts could have continuously occupied sites in such close proximity over thousands of years); 2) the apparently earlier loss of carnivores relative to horses (*Hippidion saldiasi*), *Lama cf. owenii*, and mylodonts; 3) the disappearance of horses and *L. cf. owenii* near the time dominant vegetation transforms from grasslands to increasingly dense *Nothofagus* forest; 4) and the loss of mylodonts only after dense *Nothofagus* forests established.

This pattern is most consistent with a model that sees: 1) megafauna thriving near the UEIL margins during the LGM and colonizing the newly deglaciated terrains following the ice front or proglacial lake margins of Lago Puerto Consuelo and colonizing our study area after Cerro Benítez and Cerro Señoret became broadly connected to the mainland; 2) humans arriving and ephemerally co-existing with the abundant megafauna in a cool late glacial climate dominated by grasslands; 3) loss of the carnivores through exclusion by humans; 4) loss of horses and *L. cf. owenii* as grasslands rapidly transformed into *Nothofagus* forest, reducing their preferred open-landscape habitats, and potentially as human population sizes, or frequency of visits to the area, increased and exerted more hunting pressure at the same

time; and 5) loss of mylodonts due to grassland habitat loss once *Nothofagus* forests finally became dominant.

Consistent with this model are the apparent dietary preferences of *Lama cf. owenii*, *Hippidion saldiasi*, and mylodonts. All three of these taxa preferred grasses, as inferred from dental characteristics and, in the case of mylodonts, from abundant dung samples in Cueva del Milodón (Moore 1978, Markgraf 1985, Bargo et al. 2006, Fariña et al. 2013). Also, despite some assertions that carnivore extinctions during the LQE resulted from the disappearance of their prey base (Barnosky 1989, Owen-Smith 1989, Haynes 2002, Cione et al. 2003), other ecological models may be more consistent with our observation of earlier disappearance of carnivores. Humans too are meat-eating megafauna; thus, once they enter into a new ecosystem they utilize the same prey base as other mega-carnivores. Once human numbers/visits reach a critical threshold, it is not unlikely that people would command enough of the prey base to cause population crashes in other large carnivores. Moreover, in historic and modern ecosystems where humans interact with carnivores, they selectively kill large carnivores in an effort to protect both themselves and the large herbivores they depend upon (Musiani and Paquet 2004, Alagona 2013). The biggest carnivore that persists in the Última Esperanza region today is *Puma concolor* which, compared with the two large extinct carnivores is much smaller (*Smilodon*: 350–405 kg [Anyonge 1993, Fariña et al. 1998]; *Panthera onca*: 120 kg [Prevosti and Vizcaino 2006]; *Puma*: 25–68 kg [Chester 2008]) and usually avoids direct conflict with humans.

This hypothesis rests in part on the assumption that humans and mega-carnivores consume the same prey items. In the Última Esperanza region, there is good evidence that ancient humans and ancient felids exploited at least some of the same extinct megafauna taxa. Evidence of human consumption of *Hippidion saldiasi* and *Mylodon* is found in Cueva Lago Sofia 1, as bones belonging to these two taxa, and others from extant faunas, were found in association with lithic material and hearths, and are reported to display cut marks (Prieto 1991, Alberdi and Prieto 2000, Jackson and Prieto 2005). At Cueva del Medio, burnt bones of *Hippidion saldiasi* and *Lama cf. owenii* are found along with remains of *Mylodon* and in association with hearths and lithics including fishtail projectile points, and cut marks have been identified on the horse bones (Nami and Menegaz 1991, Alberdi and Prieto 2000, Martin 2010). On the other hand, sites identified as carnivore dens (Cueva Lago Sofia 4 and Cueva Chica) offer a good source of evidence for mega-carnivore consumption of some prey items such as *Lama gracilis*, *Mylodon*, *Vicugna* and *Hippidion saldiasi* as revealed by taphonomic studies and isotopic analyses (Borrero 1997, Martin 2008, Martin et al. 2013, Prevosti and Martin 2013).

The model we suggest above implies that the chief cause of the mega-carnivore extinction resulted primarily from human impacts, with the mega-carnivores able to co-exist with people only as long as human population sizes/visits remained below a critical threshold. In contrast, the available evidence indicates that the key driver of extinction of horses, *Lama cf. owenii*, and mylodonts was climate-driven vegetation change which reduced the availability of open environments. It may well be that growing human population sizes around the time of the vegetation change exacerbated the

decline of the megafauna herbivores at that time, but so far the data are not available to robustly quantify human population growth through the critical time intervals in Última Esperanza. Human impacts combined with a reduction of open areas as a driver of the megafaunal extinction in South America has been discussed in earlier works (Cione et al. 2003).

The role of humans in changing vegetation structure through the use of fire has been proposed as a possible driver of megafauna extinction, especially in Australia (Miller et al. 1999). In the case of Última Esperanza, climate changes and the consequent changes in vegetation and wood fuels have been proposed as the main factor leading to the fire frequency increases recorded at Lago Eberhard and Pantano Dumestre (Moreno et al. 2012), a pattern that has been reported for other sites of southern South America (Whitlock et al. 2007). While the role of humans as providers of the ignition source and causing then an important impact on the vegetation is still an open possibility, our data analysis does not support that hypothesis, mainly because the observed changes in vegetation do not fit the expectations from widespread human-induced fires in the region (Vidal and Reif 2011). The extinction chronology summarized in Fig. 4 also highlights potential correspondence between the last appearance of *Vicugna vicugna* in the Última Esperanza region, the Antarctic Cold Reversal, and the eruption of the Reclús volcano. It may be that one or both of these factors decimated what may have been a small population of *V. vicugna* at that time, but given that there are only three dates on the taxon, it is impossible to draw any firm conclusions. Other specimens identified as *Vicugna* and radiocarbon dated to 12 564 cal yr BP have been found in the site Tres Arroyos 1 located in Tierra del Fuego, more than 300 km to the south east of Última Esperanza (Massone and Prieto 2004, Weinstock et al. 2009), suggesting that this taxon could have persisted longer, at least in that area of Patagonia. The Reclús eruption, though producing widespread ash, does not seem to correspond with the loss of any of the other megafauna.

Lama gracilis is known by only a single date. Therefore, at this point nothing definitive can be said about that taxon's disappearance, but the date does verify that megafauna occupied the Última Esperanza region very shortly, and/or very sparsely, after it became ice-free.

There is the possibility that the changes in vegetation observed in Última Esperanza could be the result of herbivore release due to the extinction of the megaherbivores, as has been proposed for other regions of the world (Rule et al. 2012, Gill 2014, among others). However, that is not supported by the data presented here. The herbivores that became extinct in the area were mainly grazers, specializing on grasses in open habitats, so were not likely to exert a control over forest growth by direct consumption. *Mylodon*, the biggest herbivore that could have had the capability to influence the growth of *Nothofagus* by trampling, felling trees or carving pathways, did not become extinct until long after the major expansion of *Nothofagus* was underway.

Conclusions

A detailed compilation of robust radiocarbon dates on megafauna from the Última Esperanza region, compared with

archaeological dates and existing pollen and paleoclimate data, helps to elucidate the causes of the Late Quaternary Extinction event in Chile's southern Patagonia. Megafauna colonized the region fairly soon after glaciers retreated and ancient pro-glacial lake Lago Puerto Consuelo margin was low enough ($\sim > 120$ m a.s.l.) to leave habitable land open after ~ 18 thousand yr ago. Humans arrived 4000 yr later and co-existed, at least ephemerally, for several millennia with most of the megafaunal taxa living in the area. The chronology of extinction of different genera compared to the timing of climate and vegetation change reveals that extinction of the mega-carnivores *Smilodon* and *Panthera* likely slightly preceded extinction of the most abundant megaherbivores (*Hippidion saldiasi* and *Lama cf. owenii*; and almost certainly the mylodont sloths). We suggest that humans caused the mega-carnivore extinctions, either by indirect interactions via commandeering more of the megaherbivore prey base once human population sizes/visits reached critical mass/frequency, or by targeting carnivores directly to make the region safer for humans, or a combination of both. *Hippidion saldiasi*, *Lama cf. L. owenii*, and mylodont sloths all drop out of the record coincident with major vegetation changes that were triggered by end-Pleistocene climate changes. The first two disappear as grasslands begin to rapidly transform to *Nothofagus* forest and mylodonts drop out once dense *Nothofagus* cover is fully established. This correspondence points to environmental change that resulted in the loss of their preferred grassland habitats as a key driver of these taxa's demise, although it may be that growing human population sizes exacerbated the pressures; adequate data on human-population growth/frequency of visits is not available for the crucial time period. *Vicugna vicugna* may have been extirpated from the region coincident with some combination of the eruption of the Reclús volcano and the Antarctic Cold Reversal, but with only three dates on the taxon it is not possible to come to definitive conclusions as to cause of its demise (and with the large confidence bands on the estimated times of extinction, by chance alone any volcanic eruption is likely to overlap with one or more times of plausible extinction).

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