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Relationships between terrestrial animal exploitation, marine hunter-gatherers and palaeoenvironmental conditions during the Middle-Late Holocene in the Beagle Channel region (Tierra del Fuego)

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ABSTRACT

Palaeoenvironmental information collected from zooarchaeological (guanaco exploitation) and palynological (pollen and fungal remains) records from Tierra del Fuego and Isla de los Estados allowed us to reconstruct the natural scenarios during the Holocene to better understand the human behavioral patterns and cultural changes. We have seen that changes in subsistence and guanaco exploitation would not have necessarily been synchronous with climatic variations. However, there is evidence of great climatic and environmental variability in the Fuegian Archipelago during the last 6000 years that would have influenced the distribution of the hunter-gatherer societies. In particular, the Little Ice Age (LIA) event could have caused a reorganization of subsistence activities of the hunter-gatherer societies. The stress caused by this severe climatic episode might have changed the availability of the guanaco population over the inland and coastal areas along the Beagle Channel. Indeed, the colder conditions would have significantly impacted on both the animal population and the availability of their food sources. In summary, the guanaco availability decreased under those colder and intense winters, which is clearly reflected in the substantial drop in the zooarchaeological record.

1. Introduction

The human use of spaces and animal resources changed over time at the Beagle Channel indicating the existence of different forms of interaction during the Holocene. Those changes were identified from zooarchaeological studies and were proposed in both the marine and terrestrial ecosystems (Zangrando, 2009; Tivoli, 2010; Tivoli and Zangrando, 2011). More recent studies addressed possible causes for these variations based on palaeoenvironmental information (Saporiti et al., 2013), prey behavior (Zangrando et al., 2014) or cultural factors (Martinoli and Vazquez, 2014; Zangrando and Tivoli, 2015; among others). These discussions were focused on the relationships between hunter-gatherer societies and marine resources. Concerning the past use of terrestrial landscapes by hunter-gatherer societies, the zooarchaeological model indicated that human groups would have experienced an expansion in the mobility ranges towards inland sectors from coastal areas since 5000 cal yr BP (Zangrando, 2009). This was suggested by the significant increase of guanaco (*Lama guanicoe*) bone remains in the zooarchaeological assemblages in coincidence with the appearance of lithic points over the region (Laming-Emperaire, 1968; Piana, 1984; Legoupil, 2003). The large amount of guanaco bone remains and its relation with new hunting strategies was discussed on other opportunities (Orquera and Piana, 1999a; Orquera, 2005; Piana and Orquera, 2007). However, the causes of these variations are still an open debate.

In this paper we evaluate the most important palaeoenvironmental changes in the Beagle Channel area over the last 6000 years using multiproxy analyses in order to establish the correlation between this information and the main trends in the zooarchaeological record. The main aspect has therefore been to study the interaction of human, fauna, and environmental conditions during the Holocene. In particular, we are interested in exploring the use of inland space by hunter-gatherer societies during the cold periods, as potential stress events, in contrast to the events of climatic amelioration when the circumstances would have been more favorable.

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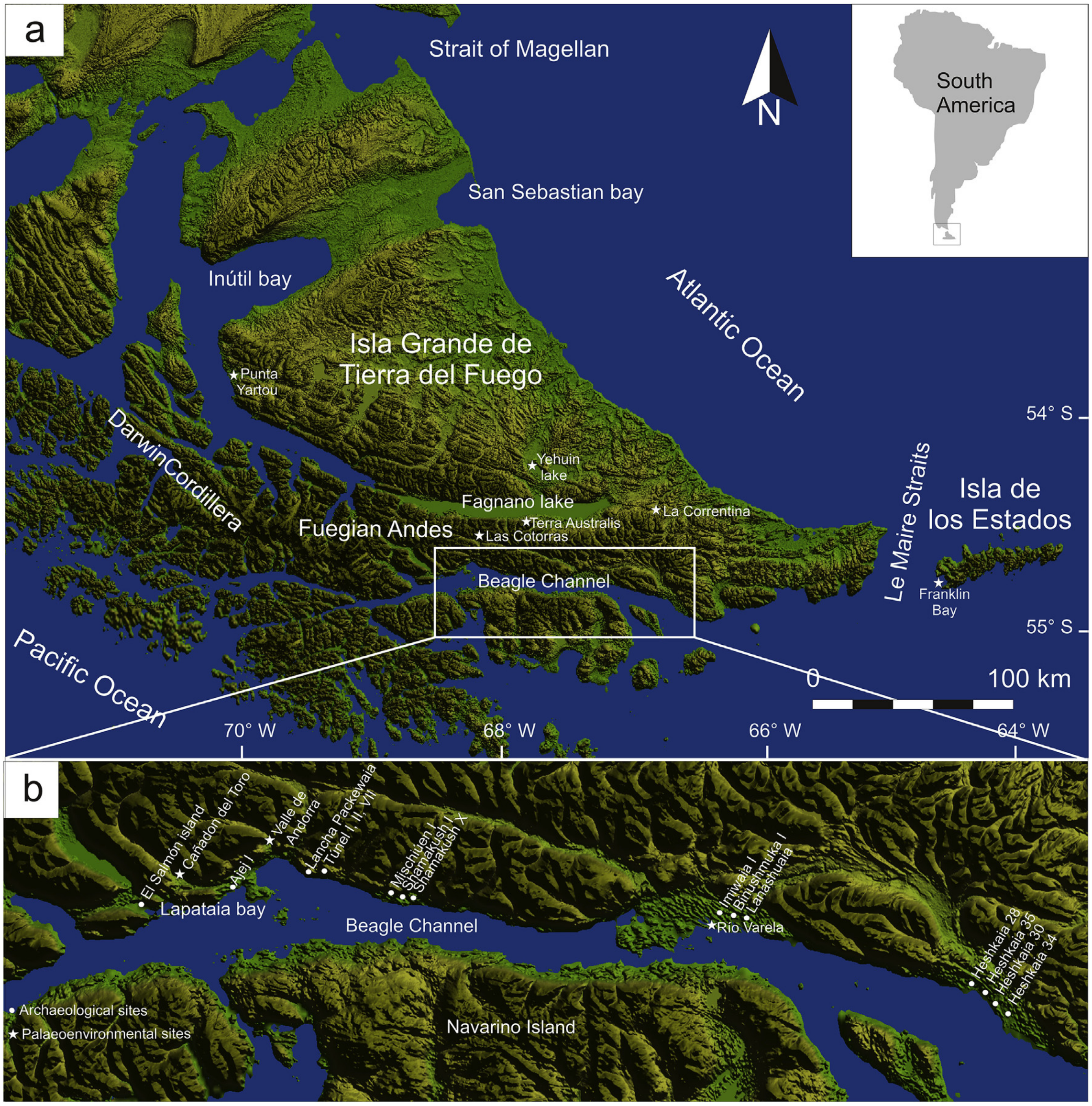

Fig. 1. (a) Map of Fuegian Archipelago showing the palaeoenvironmental sites mentioned in the text (white stars). The study area is depicted in the box. (b) Map of the study area with the location of the archaeological sites (white points).

2. Geographical setting

The landscape of the Fuegian Archipelago can be divided into two main regions: the Fuegian Andes to the south and west, and the high plains to the north (Fig. 1). The Fuegian Cordillera forms a mountain system with a W–E (south) and NW–SE (north) orientation, with decreasing elevation from W to E and from S to N. These are the lowest Andean summits in Patagonia. The maximum elevations are at Monte Darwin (2488 m asl) in the Darwin Cordillera. Isla de los Estados represents the southeastern end of the Fuegian Andes. The landscape of the Isla Grande de Tierra del Fuego was modified by several discharge outlet glaciers that flowed down from the Darwin Cordillera mountain ice sheet. At various times, glacier advances extended far beyond the eastern slopes into the plains, sometimes for several hundreds of kilometers (Coronato et al., 1999).

The climate of the Fuegian Archipelago is determined by its upper middle-latitude location in the belt of prevailing Southern Westerly Winds (SWW), in the path of eastward moving cyclones, not far from the Antarctic ice. The latitudinal position and strength of the SWW are controlled by the intensity and latitudinal shifts of the subtropical high-pressure cells in the Pacific and the circum-Antarctic low-pressure trough (Tuhkanen, 1992). The regional climate is highly oceanic in the west and south sectors of the archipelago, and increasingly continental towards the east and north. The regional climate is cold humid oceanic in the center and south, and cold subhumid oceanic towards the north, with a mean annual temperature of 5 °C. Precipitation is of the orographic type, provided by the most frequent winds, coming from the south and southwest (Rabassa et al., 2000; Coronato et al., 2008). Rainfall shows a strong gradient from the southwest (2000 mm yr^{-1}) to the northeast (less than 300 mm yr^{-1}) (Tuhkanen, 1992). A west-east precipitation gradient is also evident with 1000 mm yr^{-1} at the easternmost tip of Tierra del Fuego and close to 2000 mm yr^{-1} in Isla de los Estados (Ponce et al., 2011).

Vegetation composition reflects the strong *trans*-Andean climatic and topographic gradients (Moore, 1983; Tuhkanen, 1992) (Fig. 2). Subantarctic Deciduous Forest is represented by two species of southern beech *Nothofagus pumilio* (lenga) and *N. antarctica* (ñire), which grow from sea level to an average altitudinal limit of 550–600 m asl, and become dominant where the precipitation exceeds 450 mm yr^{-1} (Pisano, 1977; Moore, 1983). Towards the south and west of Tierra del Fuego, the annual precipitation rises to over 700 mm and Subantarctic Evergreen Forest develops, which is dominated by *N. betuloides*

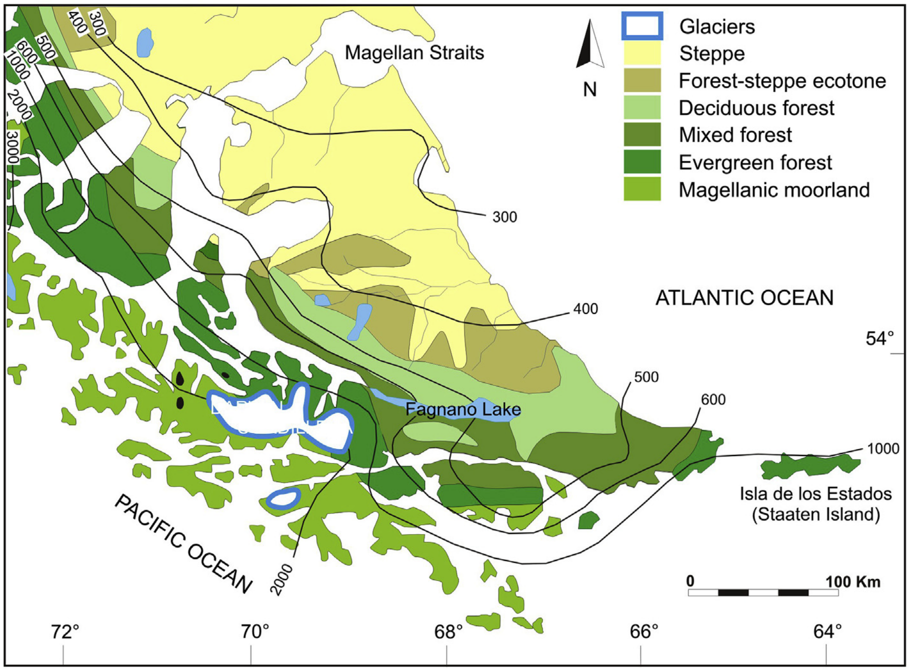

Fig. 2. Modern-day vegetation map of the Isla Grande de Tierra del Fuego with the mean annual precipitation isohyets (modified from Tuhkanen, 1992).

(guindo), accompanied by *Drimys winteri* (canelo), *Maytenus magellanica* (maitén), and abundant ferns and mosses (Moore, 1983). Initially, *N. betuloides* is intermingled with *N. pumilio* in an association known as Mixed Evergreen-Deciduous Forest which can be considered as ecotonal between the two communities (Moore, 1983). Magellanic moorland occurs beyond the forest along the exposed outermost coast under conditions of increased precipitation ($> 1500\,mm\,yr^{-1}$), high winds and poor drainage. It consists of a mosaic of barren rock, marginal grassland, cushion bogs, scrub, and fragments of evergreen forest (Moore, 1983). Above the treeline in the Fuegian Cordillera, Andean tundra is comprised of cushion plants, dwarf shrub heaths, and meadow communities (Pisano, 1977; Heusser, 2003). Isla de los Estados is characterized by the presence of exuberant vegetation dominated by Subantarctic Evergreen Forest and Magellanic moorland (Ponce et al., 2017).

3. Principal palaeoenvironmental events during the Middle-Late Holocene

3.1. Holocene marine transgression into the beagle channel

The climate improvement in Tierra del Fuego during the Early Holocene was coincident with a eustatic transgressive event into the Beagle Channel, which took place around 8500 cal yr BP (Rabassa et al., 1986; Candel and Borromei, 2016). The incoming seawater flooded the area of Lago Roca-Bahía Lapataia (at the western end of the channel) generating a deep and wide fjord with intricate archipelagos (Gordillo et al., 1992). Several authors indicate the existence of a differential tectonic uplift in the Beagle Channel during the last 8000 yr (Gordillo et al., 1992; Rabassa et al., 2000; Isla and Bujalesky, 2008; Bujalesky, 2011). The uplift would have been higher at the western end of the channel (approximately $1{,}2 \pm 0{,}2\,mm\,yr^{-1}$), decreasing toward the east. The combination of the tectonic uplift and the eustatic transgressive–regressive event generated several raised marine deposits. The curve of the relative sea level in the Beagle Channel showed a maximum between 6000 and 5000 ^{14}C yr BP (6800 and 5700 cal yr BP) (Gordillo et al., 1992). During the marine incursion into the channel, the littoral vegetation was mainly arboreal, suggesting high effective moisture due to the moderating action of the sea. The pollen records from marine levels, dated between 8478 and 7526 and 5978 cal yr BP at Bahía Lapataia (Fig. 1b), and at 6440 cal yr BP at Río Varela (Fig. 1b), showed a significant increase in *Nothofagus* pollen suggesting the development of a closed-canopy forest along the coastal areas (Grill et al., 2002; Borromei and Quattrocchio, 2007; Candel and Borromei, 2016). Inland, the landscape showed the physiognomy of a forest-steppe ecotone during the time of the marine transgression, in concordance with the regional vegetational pattern (Musotto et al., 2016). After ca. 7000 cal yr BP, the closed-canopy *Nothofagus* forest established along the Beagle Channel area and the intense fire activity that characterized the Early Holocene times declined due to an increase in effective moisture (Borromei et al., 2016; Musotto et al., 2016).

3.2. Impact of the Hudson (H_1) volcanic eruption

Several tephra layers, regionally widespread in southernmost Patagonia, provide evidence of frequent explosive volcanic eruptions during the Late glacial and Holocene times (Stern, 2008). Most remarkable in Tierra del Fuego is the identification of a green-brown tephra layer that occurs in soil profiles, peatlands, and alluvian and lacustrine deposits (Borromei et al., 2010, 2016; Menounos et al., 2013; Walmann et al., 2014; Musotto et al., 2016, 2017a). According to geochemical and petrological analyses, this tephra was derived from a large explosive eruption (H_1) of the Volcán Hudson (45° 54′ S; 72° 58′ W, 1905 m asl), and was regionally dated 7960-7423 cal yr BP (Stern, 2008). This volcano is located at the southern end of the Andean Southern Volcanic Zone (ZVS, 33°–46° S), > 900 km further northwest from the Beagle Channel. The mid-Holocene tephra (H_1) deposition in Tierra del Fuego and Isla de los Estados (Unkel et al., 2010) probably could have caused a change in the vegetational composition. In the pollen records from the Cañadón del Toro (Borromei et al., 2016), Terra Australis (Musotto et al., 2017a), La Correntina (Musotto et al., 2016), and Lago Yehuin (Markgraf, 1983) sites (Fig. 1a), the abrupt decline in the total pollen concentration values has been interpreted as a result of the instantaneous deposition of the thick H_1 tephra layer. This process probably resulted in an increased mineralization of organic matter by microbial activity and an alteration in the trophic and water environment. Thus, the development of new suitable habitats for pioneer plants was manifested by increases in grasses, herbs, scrubs and sedges. At La

Correntina (Musotto et al., 2016) and Lago Yehuin (Markgraf, 1983) the vegetation changes clearly preceded the volcanic activity. After ca. 8600 cal yr BP, the expanse of grass, herb and shrub communities indicated conditions of decreased precipitation of < 400 mm annually if compared to the present vegetation. In western of Tierra del Fuego, Mansilla et al. (2016) identified a significant reduction in the forest cover at Punta Yartou (Fig. 1a), along with high values of charcoal which suggested an intense arid phase after ca. 8080 cal yr BP.

3.3. Neoglaciations

The Neoglaciations (= Holocene glaciations) have been recognized in some sectors of the Patagonian Andes (Mercer, 1968, 1982; Rabassa et al., 1984). Although their chronology is still not well defined, the dendrochronological (Villalba, 1990) and geomorphological studies (Rabassa et al., 1992) carried out in the Patagonian Andes indicated the existence of at least five fluctuations during the Holocene related to climatic oscillations.

In Tierra del Fuego, there is no evidence of any important neoglacial advances prior to the LIA event. Menounos et al. (2013) reported geological evidence for one or more advances of glaciers in hanging valleys of the Fuegian Andes sometime between 7960 and 7340 cal yr BP and 5290-5050 cal yr BP to limits that are only tens of meters beyond the LIA maximum positions.

The pollen records from localities along the Beagle Channel and Isla de los Estados do not show any clear evidence of the Holocene glacier fluctuations. However, at Puerto Harberton, at the eastern mouth of the channel, the intervals of a low influx of *Nothofagus* at 6380–5000 cal yr BP, 2334–360 cal yr BP and also recently, appear to bear a relationship to cooler episodes (Heusser, 1989). The first interval of decline in the arboreal influx at Puerto Harberton could be related to one of the glacier advances reported by Menounos et al. (2013). However, further study is required to confirm them. Maximum arboreal concentration values recorded after ca. 4900 and 4500 cal yr BP in southern Tierra del Fuego (Beagle Channel area) (Heusser, 1989, 1998), and after ca. 4000 cal yr BP in Isla de los Estados (Ponce et al., 2011), indicated high effective moisture related to a strengthening of the westerlies at these high latitudes (Ponce et al., 2011; Björck et al., 2012). On the other hand, low surface seawater temperature (SST) was reported from the Beagle Channel. According to Obelic et al. (1998) the SST was 1.5 °C below the present temperature between 3800 and 3500 cal yr BP., based on the isotopic composition (δ 18O) of *Mytilus edulis* shell from archaeological shell middens.

The pollen records from Isla de los Estados (Ponce et al., 2011; Björck et al., 2012) show that the highly cold, humid conditions ended when the *Nothofagus* pollen declined abruptly after ca. 3000 cal yr BP suggesting warmer and drier conditions perhaps due to a weakening of the westerlies. This change has also been recorded in the pollen record from the Lago Fagnano area (Musotto et al., 2016), where the closed-canopy forest was replaced by an open *Nothofagus* forest accompanied by the development of mesic grasslands (Poaceae, *Caltha* and Cyperaceae), dwarf shrub heath (*Empetrum rubrum*) and cushion heath (*Azorella* and *Drapetes muscosus*). Climate amelioration was observed for the Beagle Channel with an increase in the SST shortly before 3000 BP (Obelic et al., 1998).

3.4. Medieval climate anomaly and little ice age

Two climatic anomaly events occurred during the last millennium, the so-called Mediaeval Warm Period (also named Medieval Climate Anomaly, MCA, 1100-800 cal yr BP (calendar years before present, present = AD, 1950)), 750–1350 AD) and the Little Ice Age (LIA, 600-100 cal yr BP, 1350–1850 AD) (Moreno et al., 2014).

The MCA date range was based on Northern Hemisphere extra-tropical tree-ring data (Esper et al., 2002). The extent, timing, and nature of the MCA are uncertain. According to Broecker (2001), evidence for a global MCA is circumstantial and the palaeoclimatic data are relatively scarce in the Southern Hemisphere. For these reasons, Crowley and Lowery (2000) suggested that the term MCA should be restricted only to the Northern Hemisphere. There is little mention of MCA in the pollen records from Tierra del Fuego. Mauquoy et al. (2004) mentioned a period of low local water table in the Valle de Andorra peat-bog (in an interior Fuegian Andes valley) between AD 1020–960. Waldmann et al. (2010) recognized the MCA in a sedimentary core from Lago Fagnano, due to low iron content intervals interpreted as representing decreased precipitation coupled with glacier retreat. At Bahía Franklin, in Isla de los Estados, reduction in the forest between 1000 and 500 cal yr BP has been related to the MCA (Ponce et al., 2011).

The LIA comprises a period in which glaciers in the mountain areas of the world were generally more extensive. In the region of the Fuegian Andes, this event was one of the most extended neoglacial advances (Menounos et al., 2013). It was identified in the pollen records from Tierra del Fuego (Heusser, 1989; Borromei et al., 2010, 2016; Musotto et al., 2016) and Isla de los Estados (Ponce et al., 2017). In La Correntina peat-bog, located in the southeastern tip of Lago Fagnano, the decline in the frequency and concentration values of arboreal taxa along with an increase in *Empetrum rubrum* and *Azorella* pollen by about 400 cal yr BP were indicative of a reduction of the *Nothofagus* forest and a drier bog surface (Musotto et al., 2016). In the interior Andean valleys, in proximity to the Beagle Channel, the *Nothofagus* forest declined during the last 1000 cal yr BP, and reached a minimum between ca. 680 and 300 cal yr BP (Borromei et al., 2010, 2016). Also, a period of cooler and/or wetter conditions between *ca.* 920-850 cal yr BP, and later at ca. 150-20 cal yr BP have likewise been recognized in the Valle de Andorra peat bog (Mauquoy et al., 2004). In Isla de los Estados, the density in the forest communities reached a minimum between ~500 and ~50 cal yr BP (Ponce et al., 2017). The decrease in *Nothofagus* pollen concentration values strongly agrees with the coolest surface water period in the Beagle Channel, at least during the last 4000 yrs (Ponce et al., 2017).

4. Human use of terrestrial landscapes

4.1. Guanaco remains as a proxy

A notable part of the biotic energy is absorbed by the formation of woody structures in the terrestrial environment of the Fuegian Archipelago. The provision of carbohydrates and proteins from plants is low (Tuhkanen, 1992), and therefore animal richness is also low. However, in spite of these low productivity conditions, guanaco was a terrestrial staple for hunter-gatherer societies, providing food and raw materials of various types (skins, bones, and tendons, among others) (Orquera and Piana, 1999b: 140–141). From what is known at present, the exploitation of this resource occurred on the coasts of Tierra del Fuego and on the Navarino island, but this hunting practice has not been archaeologically identified on other islands of the archipelago south of 54° S latitude (Saxon, 1979; Orquera and Piana, 1993–94, 1996a, 1999a,b; Zangrando, 2009; Tivoli and Zangrando, 2011; Zangrando et al., 2011; Vázquez, 2015; Alunni, 2016). This is largely because the resource would not have been available on the smaller islands south of the Beagle Channel.

The knowledge about the use of terrestrial ecosystems by marine hunter-gatherers in the Beagle Channel is still scarce, mainly because inland archaeological sites are extremely rare. The degree of interaction between those environments and the past human populations can however be assessed indirectly by the study of the frequencies and composition of guanaco bone assemblages at coastal sites. Two sources of information indicate that this interaction existed to some degree. On one hand, ethnohistorical information indicates that human exploitation of this resource would have involved extensive inland movements from the coastlines (Orquera and Piana, 1999b: 142). On the other hand, zooarchaeological studies on anatomical profiles and bone modifications have suggested that guanaco carcasses were initially processed at locations different to the residential places on the coast (Alunni and Zangrando, 2012; Vázquez, 2015; Alunni, 2016).

4.2. Guanaco bone assemblages

The NISP (Number of Identified Specimens) was used to determine the relative importance of guanaco remains in zooarchaeological assemblages from the Beagle Channel area, at the southern Tierra del Fuego. The ratios of guanaco abundances were calculated by subdividing the NISP values of guanaco remains by the aggregate NISP values of the most representative fauna at the archaeological assemblages (i.e. pinniped, bird, fish, and guanaco specimens). Canid and rodent remains were not considered due to the potential natural incorporation of these taxa to the records. Cetacean bones were also excluded because their presence in the archaeological record can mainly be explained as bone debris from instrumental production rather than as butchering activities (Smith and kinahan, 1984; Orquera and Piana, 1999a,b).

The advantages and disadvantages of NISP for deriving interpretations for human subsistence are widely known (Grayson, 1984). The main problem that has been identified for this unit is that it is biased by the degree of fragmentation and has the assumption that all specimens are equally affected by deliberate breakage. In this sense, it is important to note that butchering techniques (that partitioned bones to get nutritional contents) can overestimate the representation of guanacos versus other resources. Moreover, specimen counts may also indicate that some assemblages are the product of kill sites, while others sites with a different functionality can show that only some selected portions were introduced. However, these reasons are not sufficiently compelling to dismiss the use of NISP values for a comparative task. In spite of the fact that NISP can be differentially affected by fragmentation patterns, it is the unit of taxonomic abundance that is available for the majority of the archaeological assemblages on the south coast of Tierra del Fuego. Significant differences in the functionality were not reported in archaeological contexts of the north coast of the Beagle Channel, corresponding mainly to residential bases (Orquera and Piana, 1999a,b) and unimportant variations in butchering patterns of guanaco carcasses were identified throughout the archaeological sequence of this region. Additionally, the calculation of this unit is uniform among analysts, whereas other methods, like the Minimal Number of Individuals (MNI), may be more exposed to analytic choices made in the lab (Grayson, 1984; Lyman, 2003; among others). Therefore, we consider that NISP is an appropriate unit for the comparative purposes of this paper.

Table 1 presents the NISP values and guanaco ratios for 28 archaeological assemblages. The guanaco ratio through the last 7500 cal yr BP is shown in Fig. 3. Guanacos bones present low ratios in general: values lower than 10% are recorded for 14 assemblages, while 11 cases present guanaco ratios between 10 and 46%. Situational dominance of guanaco remains are only observed at three sites: Isla Salmón, Heshkaia 34 and Heshkaia 35 (Fig. 1b).

4.3. Archaeological background and expectations

The increase in guanaco remains reported from 5000 cal yr BP was associated with a diversification process in the subsistence strategies of hunter-gatherer populations, which took place in the Beagle Channel area (Zangrando, 2009). It was characterized by an increase in hunting activities of guanacos and small vertebrates (i.e. birds), rather than the hunting of pinnipeds. An intensification of fishing activities was also identified in later times, from approximately 1500 cal yr BP (Zangrando, 2009; Tivoli and Zangrando, 2011).

Some greater representations of guanaco remains occur at specific locations where presumably this resource was more accessible or abundant, as was proposed for the Shamakush locality on the north coast of the Beagle Channel (Orquera and Piana, 1996b) (Fig. 1b, Table 1). However, more recent excavations carried out at this locality did not show any significative guanaco remains in other archaeological assemblages (Piana et al., 2004), and therefore, they do not support this supposition. Moreover, we were also able to verify that these ungulates showed high representations at locations where its availability was supposedly scarce or less accessible (e.g., Early Component of Lancha Packewaia and Third and Fourth Component of Túnel I, Orquera and Piana, 1999a) (Table 1). The higher representation of guanaco remains at these assemblages was probably related to the appearance of new hunting technology (lithic points) around 5000 cal yr BP, but the causes of these relations are uncertain (Orquera and Piana, 1999a: 91–92; Piana and Orquera, 2007). In summary, it is still unclear why the increase in guanaco exploitation was recorded in some specific time spans in the archaeological sequence and not steadily over longer periods of time, as observed in the bone representations of small resources (birds and fishes). Indeed, this apparent discrepancy indicates that the use of guanacos and terrestrial environments by marine hunter-gatherers oscillated depending on the affordances and climatic constraints.

While the guanaco is a species with flexible dietary habits that even includes the intake of leaves of subantarctic forest trees (González et al., 2006), the winter snowfall impacts significantly on the available food substrate (Raedeke, 1978). In Tierra del Fuego, the guanaco does not have any natural predators that affect its dispersion and abundance. Its main cause of death is related to winter stress and the scarcity of food resources (Raedeke, 1978; Merino and Cajal, 1993: 136; Montes et al., 2000; Borrero, 2001a). This suggests that cold periods would have affected the availability of this resource for human exploitation in the past. At archaeological and geological time scales, these variations may have been combined with other natural events (e.g. volcanic eruptions) with similar consequences on guanaco populations.

5. Discussion

The palaeoenvironmental conditions along the Beagle Channel area were unstable as indicated by the coastal geomorphology and vegetation history. Under these circumstances, marine hunter-gatherers varied their exploitation of the resources and landscape use. Therefore, a different pattern of behavior may be correlated, or not, with the palaeoenvironmental context. Although foraging activities were mainly based on maritime resources, guanaco remains were represented particularly in coastal archaeological sites along the north coast of the Beagle Channel during the Middle to Late Holocene. The evolution of the channel from a glacial valley to a completely marine environment occurred by ca. 8500 cal yr BP (Rabassa et al., 1986; Candel and Borromei, 2016). Therefore, the possibility of the native people becoming maritime specialists was established from the Early Holocene. On the other hand, it has been argued that the onset of forest expansion was also a key factor for human marine adaptation since this environment provided raw materials, such as bark and wood, for the production of watercraft and hafts as from the Middle Holocene (Orquera and Piana, 1988, 2005).

In the Beagle Channel, coastal occupations are known from the Early Holocene: the First Component of Túnel I site, 6980 ± 100 and 6680 ± 210 ^{14}C yr BP (7942 -7590 cal yr BP) (Orquera and Piana, 1999a,b), the layer S of Imiwaia I site, 7842 ± 53 ^{14}C yr BP (8662-8420 cal yr BP) (Orquera and Piana, 2009; Zangrando, 2009; Piana et al., 2012) and the layer S of Binushmuka I site, 7486 ± 64 and 7310 ± 40 ^{14}C yr (8386-7980 cal yr BP) (Zangrando et al., 2018) (Fig. 1b). However, no bone evidence was recorded in these assemblages because of the very poor conditions for organic preservation. Human marine adaptation has been confirmed since 7500 cal yr BP as indicated by the materials recorded in the archaeological deposits such the “Second Component” of Túnel I (TISC) and the “Lower Component” of the Imiwaia I site (LCII) (Orquera and Piana, 1999b, 2009; Alunni, 2016; Vázquez, 2015). Orquera and Piana (2009) calculated that 66%

Table 1
Archaeological sites located in the southern Fuegian Archipelago and the number of identifiable specimens (NIPS) of guanaco.[1] Calib 6.0.1 (2σ − SHCal04) (Mccormac et al., 2004).

Locations (West longitude ranges)	Archaeological Sites		Radiocarbon ages	Cal yr. BP[1]	Pinníped	Guanaco	Bird	Fish	Guanaco ratios (%)	References
					NISP	NISP	NISP	NISP		
Ushuaia (68.55°–68.15°)	Isla El Salmón		1765 ± 25	1184–786	2	50	12	0	78.0	Figuerero Tórres and Mengoni Goñalons (1986)
	Ajej I		1400 ± 90	1431–1058	1011	10	499	35	0.6	Piana et al. (2008)
	Túnel I	Phase I	6470 ± 100/6020 ± 120	7515–7156	2223	149	70	39	6.0	Zangrando (2009)
	(Layer D)	Phase II	6410 ± 150	7517–6906	6645	305	252	463	4.0	Zangrando (2009)
		Phase III	5950 ± 170	7161–6393	3288	191	185	484	4.6	Zangrando (2009)
		Phase IV			11346	752	901	194	5.7	Zangrando (2009)
		Phase V	5840 ± 185/5630 ± 120	7026–6208	5067	254	450	859	3.8	Zangrando (2009)
		Phase VI	4590 ± 130	5479–4857	4764	642	515	387	10.2	Zangrando (2009)
		Phase VII			4434	830	305	1028	12.6	Zangrando (2009)
		Phase VIII			3398	618	527	404	12.5	Zangrando (2009)
	Túnel I (Third Component)		4300 ± 80	4987–4566	983	741	800	107	28.0	Orquera and Piana (1999a)
	Túnel I (Fourth Component)		2660 ± 100	2926–2376	780	1521	960	44	46.0	Orquera and Piana (1999a)
			2690 ± 80	2954–2675						
	Túnel I (Fifth Component)		1920 ± 80	2003–1691	707	318	64	19	29.0	Orquera and Piana (1999a)
			1990 ± 110	2156–1610						
	Túnel I (Sixth Component)		450 ± 60	687–510	113	10	32	233	3.0	Orquera and Piana (1999a)
			670 ± 80	718–704						
	Túnel II		1120 ± 90	1184–786	384	27	1436	0	1.0	Orquera & Piana (1986–87)
	Túnel VII		100 ± 45	100	8953	117	13727	1390	0.5	Orquera and Piana (1999a)
	Lancha Packewaia (Early Component)		4020 ± 70	4643–4228	1429	1646	608	2	45.0	Orquera & Piana (1993–94)
Remolino (68.00°–67.95°)	Mischiúen (Layer F)		4430 ± 180	5472–4521	544	1130	1156	647	32.0	Piana et al. (2004); Tivoli and Zangrando (2011)
	Mischiúen (Layer C)		890 ± 90	932–649	1942	673	1882	0	15.0	Piana et al. (2004); Tivoli and Zangrando (2011)
	Shamakush I		1020 ± 100	1066–711	102	1227	653	3006	25.0	Orquera y Piana (1996b)
			940 ± 110	990–650						
	Shamakush X		500 ± 100	574–305	9	9	191	30	4.0	Orquera and Piana (1999a)
Harberton (67.30°–67.25°)	Imiwaia I (Layers K, L and M)		5943 ± 48	6864–6625	3317	3230	1964	10187	17.0	Orquera y Piana (1999a); Zangrando (2009)
			5872 ± 147	6988–6308						
	Imiwaia I (Layer B)		154 ± 70	158–163	308	86	2164	2366	2.0	Orquera y Piana (1999); Zangrando (2009)
	Lanashuaia		XIX Century	100	69	23	219	758	2.0	Piana et al. (2000)
Moat (66.84°–66.82°)	Heshkaia 34		981 ± 36	924–772	62	613	90	56	75.0	Alunni and Zangrando (2012)
	Heshkaia 28		678 ± 38	660–554	2	11	74	18	10.0	Alunni and Zangrando (2012)
	Heshkaia 35		656 ± 35	653–548	6	834	136	66	80.0	Alunni and Zangrando (2012)
			532 ± 35	550–497						
			816 ± 35	743–660						
	Heshkaia 30		263 ± 35	223–145	21	25	444	677	2.0	Alunni and Zangrando (2012)

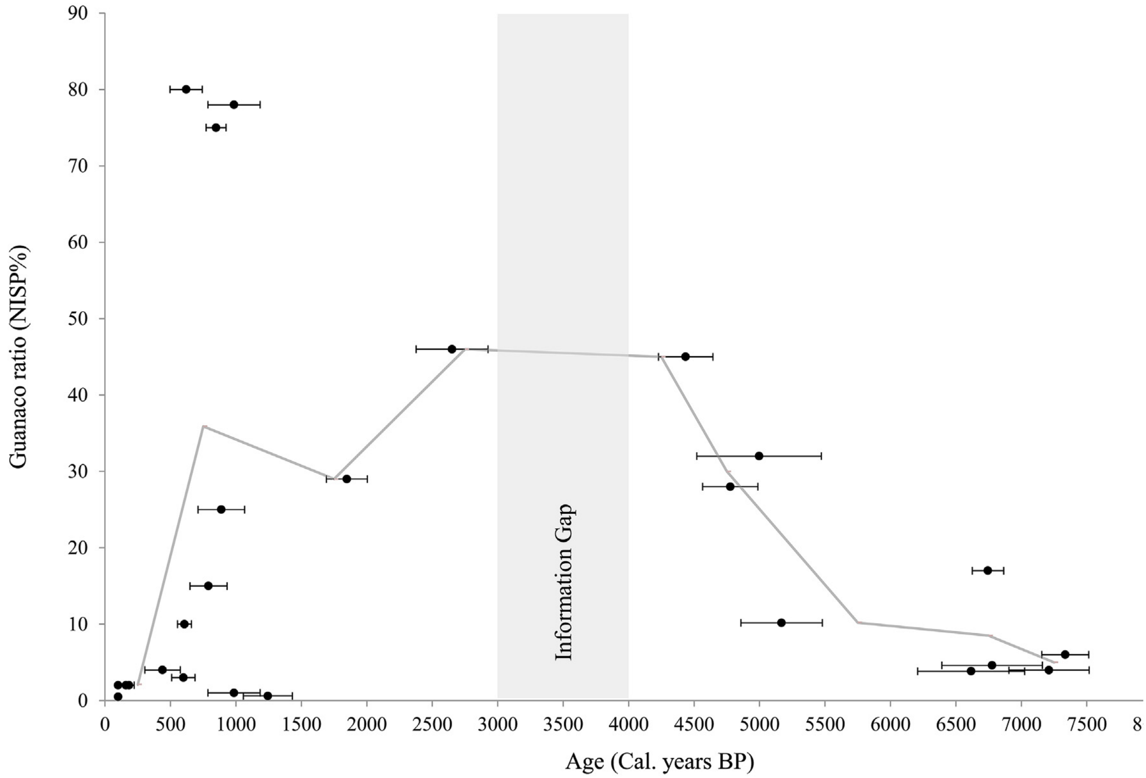

Fig. 3. Guanaco exploitation (%) through the last 7500 cal yr BP. The graph shows mean values of number of identifiable specimens (NISP) of guanaco: Black dots indicate the guanaco ratios by calibrated age ranges for each zooarchaeological assemblage; grey line shows the temporal trend from mean values estimated each 500 years.

of the calories consumed by humans in TISC site came from pinniped meat and fat, 25% from mussels, and only 5% from guanacos. In the LCII, guanaco remains are more abundant than at the aforementioned site, although they are not dominant in the assemblages.

The eruption (H_1) of Volcán Hudson (7960-7423 cal yr BP; Stern, 2008) had a great impact on the human population –interrupting long distance terrestrial transport of obsidian in southernmost Patagonia (Stern, 2004) – and palaeovegetal communities. Also, the trophic states of many water bodies were modified. Prieto et al. (2013) associated this volcanic event with the development of the human maritime adaptation in the area. For these authors, the eruption (H_1) of Volcán Hudson may have had catastrophic environmental effects on the terrestrial flora and fauna over an extended period of time, but it did not impact significantly on the marine ecosystem. Therefore, the volcanic eruption would have worked as a "significant trigger" leading the hunter-gatherer populations to adopt maritime subsistence strategies. Although, we do not have zooarchaeological evidence before 7500 cal yr BP, this proposal supposes that the terrestrial ecosystem would not have provided optimal conditions for human subsistence at moments immediately prior to that date (Fig. 4).

After the volcanic eruption, between 7500 and 5500 cal yr BP, the guanaco ratios remained stable with low values (less than 17%) (Fig. 3). This suggests that no significant inland use by maritime hunter-gatherers was recorded. Later on, between 5500 and 4500 cal yr BP, the guanaco ratios increased significantly up to 30–40% in bone assemblages (Fig. 3). The palaeoenvironmental data from interior valleys in the center and south of Tierra del Fuego (Borromei et al., 2016; Musotto et al., 2017b), and also from Isla de los Estados (Ponce et al., 2011), showed wetter conditions related to an intensification of the SWW after 5500 cal yr BP. These highest precipitations would have favored the development of frequent storms. In turn, such severe paleoenvironmental conditions for seafaring could have promoted guanaco hunting as a less risky activity on land. In this sense, the use of terrestrial resources such as guanaco and its exploitation in the interior valleys of Tierra del Fuego could have been a safer mode of subsistence and the guanaco would have been considered as a food reinforcement (Fig. 4). In an interesting way, technological innovations appeared at this time, coinciding with the occurrence of lithic points in the archaeological record (Orquera and Piana, 1999a, 2005, 2009). The most humid conditions recorded in southern Tierra del Fuego from 7000 to 6500 cal yr BP (Heusser, 1989; Markgraf and Huber, 2010), and Isla de los Estados from 5500 cal yr BP (Ponce et al., 2011), led to the development of denser forests, which could have affected the carrying capacity of the guanacos (Montes et al., 2000) and generated a reduction in the availability of this resource. In addition, there is a zooarchaeological gap between 4500 and 3000 cal yr BP (Fig. 4). At the upper treeline site, Las Cotorras, there are no records of coprophilous fungi, indicative of herbivorous grazers during this interval (Borromei et al., 2010). However, at low-elevation sites, like Terra Australis located south of the Lago Fagnano coast, the finding of dung fungus *Sordaria*-type at ca. 4000 cal yr BP (Musotto et al., 2017a) suggests the development of more suitable habitats for large herbivores in the lowlands than in the high Andean valleys when cold and wet conditions prevailed (Fig. 4).

Between 3000 and 2000 cal yr BP, the guanaco exploitation ratios maintained relatively high values (30–47%) in the bone assemblages (Figs. 3 and 4). At this time, the palaeoenvironmental conditions changed, according to the pollen data from Tierra del Fuego (Musotto et al., 2017b) and Isla de los Estados (Ponce et al., 2011). The forest communities became more open, accompanied by the spread of grass and shrub vegetation under drier and probably warmer conditions than before. In line with the opening of the canopy, at the Terra Australis mire around 2500 cal yr BP, the occurrence of coprophilous species, such as *Sporormiella*-type, indicated the presence of herbivorous animals in the area (Fig. 4). Also, the record of *Gelasinospora* sp. has been associated with relatively dry conditions related to the steppe

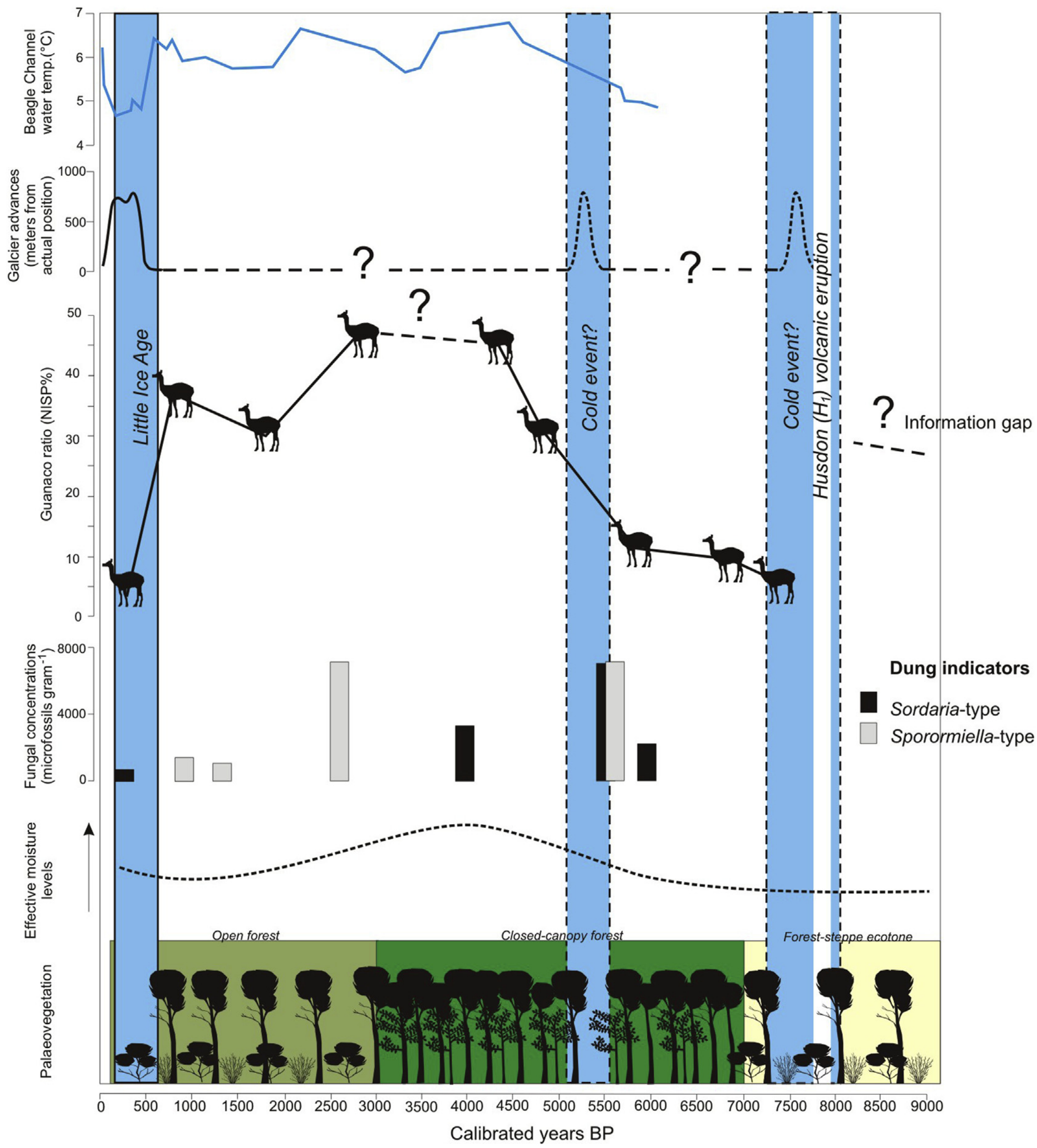

Fig. 4. Palaeovegetation pattern, effective moisture levels, coprophilous fungi concentrations from Terra Australis mire, guanaco ratio from archaeological sites, glaciers advances and Beagle Channel water temperature during the Middle-Late Holocene in the southern Tierra del Fuego. The blue vertical rectangles indicate the inferred cold periods, the white vertical rectangle indicates the Hudson (H_1) volcanic eruption, and the question marks indicate a gap of information. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

communities (Musotto et al., 2017a). *Gelasinospora* species are ubiquitous, being terricolous, carbonicolous and lignicolous, with only a few coprophilous species (Cai et al., 2006; van Geel and Aptroot, 2006). During this time, the decline in Microthyriaceae is noticeable. These latter fungal microfossils are recorded as being associated with forest communities and are well correlated with humid climates and heavy rainfall (Musotto et al., 2017b).

Between ca. 1200 and 800 cal yr BP, the guanaco ratios reached the maximum values (25–78%), but there were also cases represented by low and moderate percentages (less than 25%) (Figs. 3 and 4). The palaeoclimate data from southern Tierra del Fuego (Mauquoy et al., 2004; Walmann et al., 2014) and also from Isla de los Estados (Ponce et al., 2011) indicated a decrease in the precipitation coupled with the opening of the forests probably under mild and warm conditions linked to the MCA event. In Terra Australis mire, *Sporormiella*-type and *Glomus* sp. were recorded along with a decline in Microthyriaceae and *Byssothecium* sp., all indicative of low-humidity environments related to open ground vegetation and the presence of herbivorous grazers in the area (Fig. 4) (Musotto et al., 2017b).

By 600 cal yr BP, the guanaco exploitation (< 4%) abruptly declined (Fig. 3). The pollen data from the interior Andean valleys, in the proximity of the Beagle Channel, showed a drastic drop in the *Nothofagus* pollen frequencies, reaching a minimum between ca. 680 and 300 cal yr BP (Borromei et al., 2010, 2016). Also, the pollen records displayed a similar pattern in the center of Tierra del Fuego (Musotto et al., 2016) and Isla de los Estados (Ponce et al., 2017). Possibly, the climate would have been as cold and windy as to inhibit the *Nothofagus* trees growth in the Fuegian Andes zones. Chambers et al. (2014) also found an intense dry episode associated with the LIA event in the Valle de Andorra (an interior Andean valley) that was attributed to solar-driven changes in atmospheric circulation, and more specifically to a shift in the geographical position of the westerlies. Nowadays, a sharp drop in mean air temperature is associated with southerly air flow that drives sub-antarctic air towards southern Patagonia (Schneider et al., 2003). The stress caused by these severe climatic conditions related to the LIA event might have changed the availability of guanaco populations over the inland and coastal areas along the Beagle Channel (Fig. 4). Also it is noticeable that dung fungi were not recorded either in the upper treeline site, Las Cotorras, or in the low-elevation site, Terra Australis, during this event. Indeed, colder conditions over an extended period of time would have impacted significantly not only on the animal population but also on the availability of their food sources (Montes et al., 2000). In summary, it is possible to suggest that the guanaco availability decreased under colder, intense winters, which is clearly reflected by the substantial drop in the zooarchaeological record.

The zooarchaeological assemblages left by the marine hunter-gatherers might indicate an expansion in the spatial ranges of foraging, integrating new areas of exploitation and incorporating some resources in the subsistence patterns (Tivoli and Zangrando, 2011). The correlation between the use of the interior valleys of Fuegian Andes and the palaeoenvironmental conditions suggest a certain grade of correspondence between them; the abrupt decline in the exploitation of guanaco after the LIA event is clear evidence of such circumstances. Taken together, these palaeodata also show that marine hunter-gatherers must have faced environmental pressures and stressful periods, but in most of the situations they showed resilience and long-term sustainability to environmental changes.

6. Conclusions

The study of relationships between terrestrial animal exploitation, marine hunter-gatherers and palaeoenvironmental conditions in the southern tip of South America is important for improving our knowledge and understanding of human behavior in the past, especially in use of landscapes. We have seen that changes in subsistence and guanaco exploitation would not necessarily have been synchronous with climatic variations. Although environmental changes can cause a reorganization of subsistence activities, it is also possible to get different human subsistence responses under the same environmental scenario. However, the possibility of comparing the results of the fungal and pollen analyses with the models of guanaco exploitation by marine hunter-gatherers gives us new insights for discussing this kind of problem.

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