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Late Pleistocene ecological, environmental and climatic reconstruction based on megafauna stable isotopes from northwestern Chilean Patagonia

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ABSTRACT

Stable isotope analyses have been performed on the bioapatite ($\delta^{13}C$; $\delta^{18}O$) and collagen ($\delta^{13}C$; $\delta^{15}N$) of four late Pleistocene South American megafaunal taxa (*Notiomastodon platensis*, *Equus andium*, cf. *Hemiauchenia paradoxa* and Xenarthra indet.) to evaluate paleoclimatic and paleoenvironmental conditions as well as paleoecological features of this time period. The analyzed megafauna was found at several locations in the northwestern Chilean Patagonia (38°–42°S, 74°–71°W). The bioapatite $\delta^{13}C$ values indicated the presence of C_3 vegetation ranging from forestal to woodland areas. The collagen $\delta^{15}N$ values pointed to temperate and humid ecosystems, and to the consumption of shrubs, trees, grasses and sedges. Mean annual temperatures estimated from bioapatite $\delta^{18}O_{PO4}$ values show a similarity to modern temperatures and suggested that the megafauna under study may have lived during warm stages (interstadials) of the late Pleistocene. When comparing our results with those obtained from other South American regions, we find that the diet of this particular Chilean megafauna appears to have been more influenced by resource availability than by the potential dietary range of the taxa.

1. Introduction

Studies of the vegetation of northwestern Patagonia (NP) at the end of the late Pleistocene indicate that during this time the region was cooler and wetter than it is today (Moreno et al., 2015). In the southern hemisphere, however, from the Last Glacial Termination (LGT = ~18 thousand years before present; kyr BP) onwards, a process of deglaciation took place (Denton et al., 2010). This leaded to the expansion of closed-canopy forests and to an increase in temperatures (Moreno et al., 2015). Approximately 20 sites with fossil mammal records have thus far been found in NP, ranging in date between ~32 and 12.5 kyr BP. They are characterized by a significant number of megafauna taxa (Gomphotheriidae, Equidae, Camelidae, Cervidae, Mephitidae, Mylodontidae and Ursidae (Pino et al., 2013) found in different states of preservation.

The data used to reconstruct the vegetation structure of the study area have primarily been obtained from pollen studies (Moreno et al., 2015 and references therein), and they constitute an important source from which to draw information on paleodiets. Pollen studies have been the essential basis in the reconstruction of the vegetation structure present in the studied area (Moreno et al., 2015 and references therein) and they constitute an important complement for the inference of paleodiets. Although there have been studies of pollen and plant macrofossils in coprolites that provide solid data regarding the paleodiet of specific taxa (e.g.,

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Mylodontidae; Velázquez et al., 2015 and Dinornithiformes; Rawlence et al., 2016), the identification of plant taxa through a pollen analysis of the sediments, contemporary to the fossil megafauna, cannot totally determine their dietary preferences. Furthermore, it must always be considered that variables such as palatability, phenotypic plasticity and/or niche partitioning are relevant for interpreting the environment of an animal. On the other hand, megaherbivores are so-called ecological modellers, which can dramatically alter a landscape (e.g., Sukumar, 2003; Barnosky et al., 2015) and possibly cause a bias in the interpretation of climate and environment based on pollen studies.

Stable isotope analyses can provide detailed information about the lifestyles and habits of animals, and are therefore a useful analytical tool when investigating ancient fauna (Koch, 1998). The isotopic signal preserved on osseous tissues provides direct evidence of the ecology and physiology of extinct animals, regardless of their taxonomy (Hedges et al., 2006; Andrews and Hixson, 2014).

In Chile, isotopic studies of Quaternary mammals have been conducted on single taxa (Aguilera, 2010; Sánchez et al., 2004; Domingo et al., 2012) and on faunal assemblages (Prevosti and Martin, 2013; López Mendoza et al., 2016). In this study, we perform stable isotope analyses on megafauna remains belonging to four taxa (*Notiomastodon platensis*, *Equus andium*, cf. *Hemiauchenia paradoxa* and Xenarthra indet.) found at the site of Pilauco (40° 36′S, 73° 07′W) (16.4–12.7 kyr BP; Pino et al., 2013, 2016). Additionally, samples of gomphotheres from 14 other sites found in the same region were also analyzed. The data obtained from the gomphotheres is considered to be essential for two reasons: i) gomphotheres are considered to be ecosystem modelers. Studies have shown that both fossil and present-day proboscideans are highly generalist herbivores, whose diet seems to be more dominated by the availability of resources in the environment than by the potential dietary range of the taxa (Zhang et al., 2016); ii) proboscideans are obligate drinkers, a fact that links isotopic ratios directly to climatic and hydrological conditions.

The stable isotopes performed here allowed us to establish dietary preferences, hydrological resources and in turn, paleoecological, paleoenvironmental and paleoclimatic conditions during the late Pleistocene in the NP.

1.1. Environmental and climatic context of the study area

1.1.1. Modern climate and vegetation

According to the classification by Luebert and Pliscoff (2006), the study area today can be classified as a closed forest formation, which is characterized by the horizontal superposition of the canopy tops and by its $\geq$ 25% canopy cover (Lara et al., 2005). This particular formation includes the following forest types: sclerophyllous, deciduous, laurisilva, evergreen and resinous conifers (Gajardo, 1994) (Fig. 1). Species of the *Nothofagus* genus dominate or co-dominate temperate rainforests, from Coastal Range to the moist slopes of the western Andean Mountains (Villagrán, 1985). Based on their floristic composition, three separate forest communities have been identified in the 40°–43°S range: the Valdivian, which occupies low elevation areas in relatively warm regions with heavy seasonal precipitation; the north Patagonian forest, which consists of communities that developed under colder and wetter conditions; and the Subantarctic forest that dominates subalpine environments covered by seasonal snow (Moreno et al., 2015). NP's modern climate is mainly determined by the position and changes of the summer Pacific anticyclone, as well as by the low-pressure area in the South Pacific, and the westerlies system. Together, they are responsible for the seasonality in rainfall patterns and they intensify the amount and regularity of rain in the south of Chile (Garreaud et al., 2013). An increase in the continentally is caused by the rain shadow effect on the Coast Range over the Central Depression. The annual temperature is the most important explanatory variable regarding the degree of forest richness in Chile, although changes in diversity are mainly associated with the precipitation degree in the north of Chile (Segovia et al., 2013). Therefore, temperatures are currently the main restricting factor for wooded environments in high altitudes in the Andean Mountains, since precipitation increases with elevation at any altitude (Lara et al., 2005).

1.1.2. Paleoenvironmental background

NP's glacial geomorphological information shows recurrent glacial conditions from ~33.6 up to ~17.8 kyr BP. Following this period, the northwestern part of the Patagonian Ice Sheet suffered an extensive recession in response to the sustained atmospheric warming (Moreno et al., 2015; Darvill et al., 2016). Most of the studies based on pollen in NP show the presence of relatively open vegetation, tolerant of the prevailing moist and cold conditions for of the ~30 to 14 kyr BP period. Specifically, the pollen records suggest the existence of irregular landscapes of Subantarctic tundra, alternated with small populations of *Nothofagus* and conifers during the Last Glacial Maximum (LGM) (Villagrán and Armesto, 2004). During the LGM summer temperatures were between 6 and 8 °C below present values and precipitation was double what it is today (Berman et al., 2016; and references therein). Even if the most accepted models on the history of vegetation of NP state that the Valdivian forest (which is more thermophilous) began to dominate low altitude areas during the early Holocene (Villagrán, 2001), the possibility that small populations of certain species locally survived the glaciations cannot be completely dismissed (Quiroga and Premoli, 2010; Segovia et al., 2012).

Although an increase in temperatures allowed the onset of the deglaciation to take place ~18 kyr BP (Denton et al., 2010); the climate nonetheless continued to be colder and wetter than today. This consensus in the paleoenvironmental records of NP is most clearly observed at the Melli Lake on Chiloé island (42°–43°S) where the paleoenvironmental record shows the dominance of temperate rainforest communities under cold and wet conditions between ~16 and 11 kyr BP (Abarzúa and Moreno, 2008). Still, this interpretation of cold conditions ought to be cautiously considered, since recent reviews (see Lamy et al., 2007; Moreno et al., 2015) point out that, in low-altitude areas, the most thermophilous elements in the north Patagonic forest – that is, a temperate closed canopy rainforest – were fully established and temperatures had approached average interglacial values by ~16.8 kyr BP. However, cold reversals between ~14.7 and 11.5 kyr BP (Antarctic Cold Reversal = ACR, and Huelmo-Mascardi Cold Reversal = HMCR) have been documented in NP (see Moreno et al., 2015; references therein; Moreno and Videla, 2016) (Fig. 2). Researchers have yet to agree on the extent and impact of these reversions on the landscape (Massaferro et al., 2014).

1.2. Significance of stable isotope analyses on mammalian bioapatite and collagen

Isotopic concentrations are set in animal tissues following metabolic and physiological processes involving fractionations in δ values (Hoefs, 2008). The bioapatite carbon isotope composition differs from its original source in the diet. This process is known to take place in ungulate mammals, in such a way that $\delta^{13}C$ values of tooth enamel bioapatite ($\delta^{13}C_{enamel}$) track the $\delta^{13}C$ values of the plants they consume ($\delta^{13}C_{diet}$), offset by ~+14‰ due to fractionations associated with carbonate equilibria and metabolic processes (Cerling and Harris, 1999). Therefore, ranges of $\delta^{13}C$ values can be estimated for herbivorous mammals in different habitats