

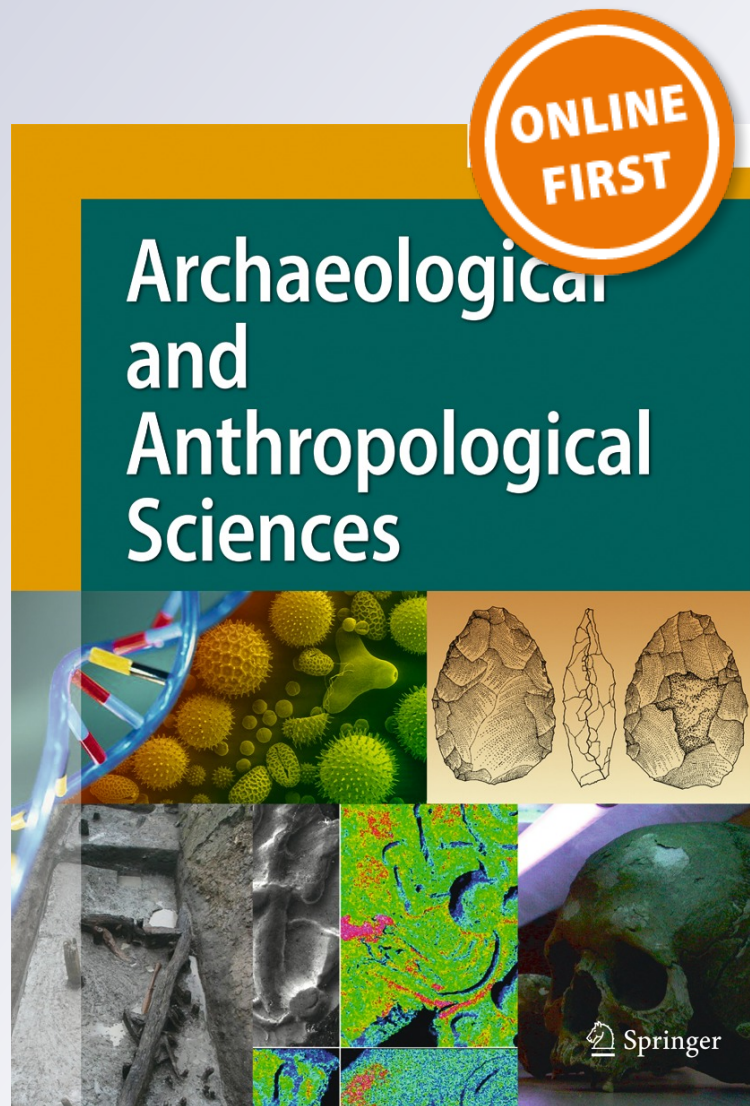
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Carbon and nitrogen isotope composition of natural pastures in the dry Puna of Argentina: a baseline for the study of prehistoric herd management strategies

Celeste T. Samec¹ · Hugo D. Yacobaccio² · Héctor O. Panarello¹

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Abstract This study represents an isotopic survey of modern plants developed to establish baseline isotopic values in order to explore prehistoric herd management strategies employed by the South American camelid herders that occupied the southern Andean highlands during the past 3000 years. We present carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic compositions of natural pastures collected from different plant communities along an altitudinal gradient in the dry Puna of Argentina. Our results show that C_3 plants are the most abundant along the whole altitudinal gradient and that C_3 and C_4 plants exhibit a differential distribution, the latter being less abundant in those sites located above 3900 meters above sea level (masl). At the same time, plants growing at low-altitude sites with low water availability exhibit higher $\delta^{15}\text{N}$ values than plants growing at high-altitude sites with higher water availability. These results explain the negative correlation found between altitude and South American camelid bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values published in previous studies. This work represents a fundamental step towards the building of an isotopic ecology for the dry Puna area with the ultimate goal to explore herd management strategies employed by human groups in the past. In this sense, modern plant and South American camelid tissue

isotopic compositions would provide a frame of reference to interpret isotopic compositions measured on archaeofaunal remains recovered at pastoral sites, with the aim to explore mobility and pastureland use by prehistoric herders.

Keywords C_3 and C_4 plants · South American camelids · Carbon and nitrogen stable isotopes · Altitude · Herding strategies

Introduction

Stable isotope analyses are frequently employed as a tool for reconstructing diet and mobility patterns of prehistoric human groups (Ambrose and Krigbaum 2003; Kellner and Schoeninger 2007; Price et al. 2012, among many others) and diet and migration patterns of prehistoric animal populations (Madgwick et al. 2013; Stevens et al. 2013; Thornton et al. 2011, among many others). Particularly, the carbon and nitrogen isotopic compositions of animal and human tissues reflect the isotopic compositions of the foods consumed (Kelly 2000; Tykot 2004). Therefore, interpretations of isotopic data from archaeological contexts depend on an accurate knowledge of the range and variation in isotopic compositions of potentially consumed food stuffs and their position in the food chain (Ambrose 1991). In the past few years, the development of studies that address the baseline variation in the isotopic compositions of soils and plants has been highly encouraged by most users of stable isotope analyses in many disciplines such as ecology or archaeology (Casey and Post 2011; Knudson et al. 2014; Post 2002; Szpak et al. 2013, among others). In fact, many studies highlight the importance of building an isotopic baseline for any study area before addressing trophic reconstructions for the past (Ambrose and DeNiro 1986; Burton et al. 2001; among others).

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Recently, several studies have explored the potential of stable isotope analysis to investigate prehistoric herding strategies in different parts of the globe (Balasse et al. 2002; Britton et al. 2008; Finucane et al. 2006; Müldner et al. 2014; Stevens et al. 2013; Towers et al. 2011, among others). In this sense, stable isotope analysis of animal tissues represents an innovative approach to investigate how human groups exploited and managed animals in the past, allowing us to address issues such as mobility and foddering, which usually escape traditional zooarchaeological or genetic techniques applied to archaeofaunal remains (Makarewicz and Tuross 2012).

Particularly in the dry Puna of Argentina, previous works have addressed prehistoric herding and hunting strategies through stable isotope analysis of animal tissues (Fernández and Panarello 1999–2001; Mengoni Goñalons 2007; Samec et al. 2014; Yacobaccio et al. 2010). Since South American camelids (SAC) represent the most important animal species for human groups in this area in both prehistoric and modern times, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been measured on domesticated and wild SAC remains recovered at different archaeological sites and interpreted using modern stable isotope values of domesticated and wild SAC as a frame of reference (Fernández and Panarello 1999–2001; Samec et al. 2014; Yacobaccio et al. 2010). Nevertheless, these applications require establishing baseline isotopic values from plant material to fully understand the causes of variation in both modern and past SAC $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Thus, the main purpose of this work is to understand the causes of isotopic variation among plants from the dry Puna of Argentina and to develop appropriate isotopic baselines for archaeofaunal and paleodietary data interpretation. Previous studies have proposed that plant species presence and relative abundances depend mostly on altitude and its effect on temperature, moisture, atmospheric pressure and solar irradiance (Cavagnaro 1988; Llano 2009; Panarello and Fernández 2002; Szpak et al. 2013; Tieszen and Chapman 1992, among others). Therefore, this study explores the variation in plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and their correlation with altitude through stable isotope analysis of natural pastures currently available for wild and domesticated SAC consumption. Particularly, we aim to explore the distribution of C_3 and C_4 plant species and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among different vegetation assemblages along an altitudinal gradient where modern SAC tissues were already sampled (Samec 2012; Yacobaccio et al. 2009). These new results will allow us to discuss $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on SAC tissues in a new light, with the ultimate goal of building an isotopic ecology for the dry Puna of Argentina to interpret archaeofaunal isotopic values. In this sense, the development of a local survey of the vegetation potentially consumed by the animals managed by the prehistoric herders that inhabited the area has enormous implications in the investigation of prehistoric herding strategies, human dietary reconstructions and palaeoenvironmental reconstructions through stable isotope analyses (Ambrose 1991; Pate 1997; Pate and Anson 2008).

Carbon isotopic composition of plants and herbivorous ungulates

Within terrestrial ecosystems, carbon enters the food web through the uptake of atmospheric CO_2 by plants during photosynthesis (O'Leary 1988). Three photosynthetic pathways exist for terrestrial plants: C_3 , C_4 , and crassulacean acid metabolism (CAM) (Ehleringer and Cerling 2002; O'Leary 1981, 1988). These photosynthetic pathways exhibit differential discrimination against ^{13}C resulting in clear differences between the $\delta^{13}\text{C}$ values of C_3 and C_4 plants (O'Leary 1981; Smith and Epstein 1971). C_3 plants, which follow the Calvin-Benson pathway, exhibit $\delta^{13}\text{C}$ values ranging from -35 to -20 ‰ with an average between -28 and -26 ‰ (Dawson et al. 2002; Tieszen 1991). These plants include trees, shrubs, temperate grasses and legumes (Cerling 1992) and dominate temperate and high-elevation environments such as those found in the southern Andes (Panarello and Fernández 2002). In contrast, C_4 plants, which follow the Hatch-Slack pathway, exhibit higher $\delta^{13}\text{C}$ values ranging from -19 to -6 ‰ with an average between -14 and -12 ‰ (Smith and Epstein 1971; Tieszen 1991). These plants include tropical- and arid-adapted grasses from warmer and saline environments (Smith and Epstein 1971) and several cultivated plants such as maize, a main crop in the southern Andes (Cadwallader et al. 2012). On the other hand, CAM (crassulacean acid metabolism) represents a third photosynthetic option by which plants can fix carbon like C_4 plants during the night but also like C_3 plants during the day and therefore exhibit $\delta^{13}\text{C}$ values intermediate to those plant species (O'Leary 1981). CAM plants include cacti, bromeliads and other succulents, which often grow in arid and semi-arid environments (O'Leary 1981; Tieszen 1994).

Environmental conditions, such as temperature, water availability, irradiance and atmospheric pressure, can influence the distribution of C_3 , C_4 and CAM plants and their $\delta^{13}\text{C}$ values. Thus, these values may vary between plants of the same photosynthetic pathway, functional group and/or species that grow under different conditions (Codron et al. 2005; Ehleringer et al. 1997; Heaton 1999; Tieszen 1991, among others). Several studies have found that the distribution of C_3 and C_4 plants is influenced by altitudinal variation, according to its effects on temperature, precipitation and irradiance (Cavagnaro 1988; Llano 2009; Panarello and Fernández 2002; Szpak et al. 2013; Tieszen and Chapman 1992; Tieszen et al. 1979). According to these studies, C_4 plants are only present at lower elevations due to increased temperature and water stress and practically disappear above a certain threshold (between 3000 and 4000 meters above sea level [masl] depending on the specific area) where these conditions are no longer found (Tieszen et al. 1979). At the same time, several studies have revealed that $\delta^{13}\text{C}$ values of C_3 plants also vary across wide altitudinal gradients in relation to altitude (Körner

et al. 1988; Marshall and Zhang 1994; Sparks and Ehleringer 1997; Szpak et al. 2013; Tieszen 1991). For instance, Körner et al. (1991) have found that carbon isotope discrimination among terrestrial C_3 herbaceous plants decreases with altitude at several places around the globe, which results in higher $\delta^{13}C$ values even for individual species within the C_3 plant range. According to these authors, this altitudinal trend in ^{13}C discrimination is caused by both temperature and atmospheric pressure variations (Körner et al. 1991). In that respect, Tieszen and Chapman (1992) have found that the $\delta^{13}C$ values measured on C_3 plants increase with altitude across an entire altitudinal gradient (between sea level and 4400 masl) in northern Chile, but those species that occurred along the driest portions of the transect presented higher values than those that grew where water stress was less severe. This latter trend is in accordance with those studies that have found that water stress causes stomatal closure resulting in higher $\delta^{13}C$ values (Farquhar and Sharkey 1982; Farquhar et al. 1987; Tieszen 1991, among others). Nevertheless, Szpak et al. (2013) carried out a survey in northern Peru and found a positive correlation between altitude (between sea level and 4000 masl) and $\delta^{13}C$ values measured on C_3 plants regardless of water availability variations. According to these authors, their results highlight the determinant role of altitude in the carbon isotope composition of C_3 plants over water availability (Szpak et al. 2013). In any case, these results highlight the complex interaction between altitude and water availability variations along altitudinal gradients in arid and semi-environments (Marshall and Zhang 1994).

All these aspects related to variation in the isotopic composition of terrestrial plants are relevant issues when dealing with the results of isotopic analyses of animal and human tissues. In the case of carbon stable isotopes, the types of plants consumed by any herbivore will be reflected in the $\delta^{13}C$ value of its tissues since a constant enrichment in ^{13}C is produced during incorporation resulting in an isotopic offset between a consumer's tissue and its diet (Schwarcz and Schoeninger 1991). This offset, which is the "isotopic discrimination factor", can vary between 1 and 5 ‰, although most investigators work with a value of 5 ‰ when dealing with free-ranging herbivore bone collagen (Bocherens et al. 1996; Kelly 2000; Koch et al. 1994; Lee-Thorp et al. 1989). Therefore, several authors have established that the carbon isotope composition of bone collagen in herbivorous ungulates is controlled by (a) the distribution of C_3 and C_4 plants and its relative abundances, (b) the selective feeding habits particular to the different species, and (c) human intervention in diet in the case of domestic animals (Koch et al. 1994; Stevens et al. 2006). As we have previously reviewed, C_3 and C_4 distribution is determined by environmental variables such as temperature, precipitation, solar irradiance among others, and thus, herbivore $\delta^{13}C$ values will indirectly reflect the manifestation of such variables (Stevens et al. 2006).

Nitrogen isotopic composition of plants and herbivorous ungulates

Within terrestrial ecosystems, nitrogen enters the food web through the absorption of nitrogenous compounds (typically NH_4^+ and NO_3^-) by terrestrial plants directly from the soil or through symbiosis with atmospheric N_2 -fixing bacteria (Ambrose 1991; Virginia and Delwiche 1982). Non- N_2 -fixing plants exhibit a wide range of $\delta^{15}N$ values depending on soil isotopic composition and growth form but are usually higher than the $\delta^{15}N$ values of N_2 -fixing plants, mostly legumes, which range between -2 and 2 ‰ (Peterson and Fry 1987; Virginia and Delwiche 1982). Overall, the $\delta^{15}N$ values of terrestrial plants exhibit a range from -5 to 20 ‰, in which the highest values are found in arid and saline environments; whereas, the lowest ones are found in wetter environments with increased rainfall and elevation (Ambrose 1991; Heaton 1987; Virginia and Delwiche 1982). In this sense, the $\delta^{15}N$ values of plants can be influenced by environmental and physiological factors including climate, soil type, water and nitrogen availability, salinity, root depth and age, among others (Amundson et al. 2003; Austin and Vitousek 1998; Evans 2001; Handley and Raven 1992; Heaton 1987; Virginia and Delwiche 1982). These factors can lead to substantial differences in $\delta^{15}N$ values (up to 10 – 12 ‰) between different plant parts and specimens of the same plant species and between different microhabitats located within the same plant community (Handley and Raven 1992; Heaton 1987; Hobbie et al. 2000). Several studies have found a strong negative correlation between rainfall and $\delta^{15}N$ values measured on soils (Amundson et al. 2003; Austin and Vitousek 1998) and plants (Hartman and Danin 2010; Heaton 1987; Swap et al. 2004; Szpak et al. 2013). Since nitrogen is assimilated by consumers along the food web with a discrimination factor of 3 – 5 ‰ at each step (Ambrose 1991; Bocherens and Drucker 2003; DeNiro and Epstein 1981), a negative correlation between rainfall and $\delta^{15}N$ values has also been found in herbivore bone collagen (Heaton et al. 1986; Murphy and Bowman 2006; Pate and Anson 2008; Sealy et al. 1987, among others) as well as other animal tissues (Hartman 2011). Initially, some authors have postulated physiological mechanisms to cope with water stress to explain the high $\delta^{15}N$ values measured on animal tissues in arid environments (see Ambrose 1991 for details on the models suggested by: Ambrose and DeNiro 1986; Schoeninger and DeNiro 1984; Sealy et al. 1987). Nevertheless, the results of both experimental and field research provide support to reject physiological explanations in favour of those that emphasise diet as the main cause of variation in nitrogen isotope composition, explaining higher $\delta^{15}N$ values in animal tissues as a result of higher $\delta^{15}N$ values in soils and plants (Ambrose 2000; Hartman 2011; Murphy and Bowman 2006). According to this, variation in the $\delta^{15}N$ values within a food web and its correlation with water availability can be

related to the relative openness of the nitrogen cycle, as well as the predominant fraction of the soil (organic or inorganic) and the nitrogenous compounds available in it (see Amundson et al. 2003; Austin and Vitousek 1998, for details). At the same time, a previous work has found that plant $\delta^{15}\text{N}$ values increase when temperature increases (Amundson et al. 2003). In turn, a positive correlation has been observed between mean annual temperature and herbivore bone collagen $\delta^{15}\text{N}$ values (Stevens et al. 2006). According to all these results, variations in the $\delta^{15}\text{N}$ values measured on bone collagen extracted from herbivorous animals can be related to spatial differences in local environments and to the influence of variables like temperature and water availability in soil and plant $\delta^{15}\text{N}$ values (Ambrose 1991; Towers et al. 2011).

However, in spite of the numerous works exploring plant and ungulate $\delta^{15}\text{N}$ values and their correlation with water availability and temperature, very little is known about the relation between these values and altitude. In this sense, Szpak et al. (2013) found a negative correlation between altitude and plant $\delta^{15}\text{N}$ values from the coast to the highlands in northern Peru. At the same time, Ambrose (1991) presented a negative correlation between altitude and plant $\delta^{15}\text{N}$ values in East Africa related to differences in water availability and temperature along an altitudinal gradient, a correlation that was also present in herbivore tissues of the same area. Both these studies show that altitude, and its effect on temperature and water availability, must be taken into account when studying $\delta^{15}\text{N}$ values variation in both plant and animal tissues.

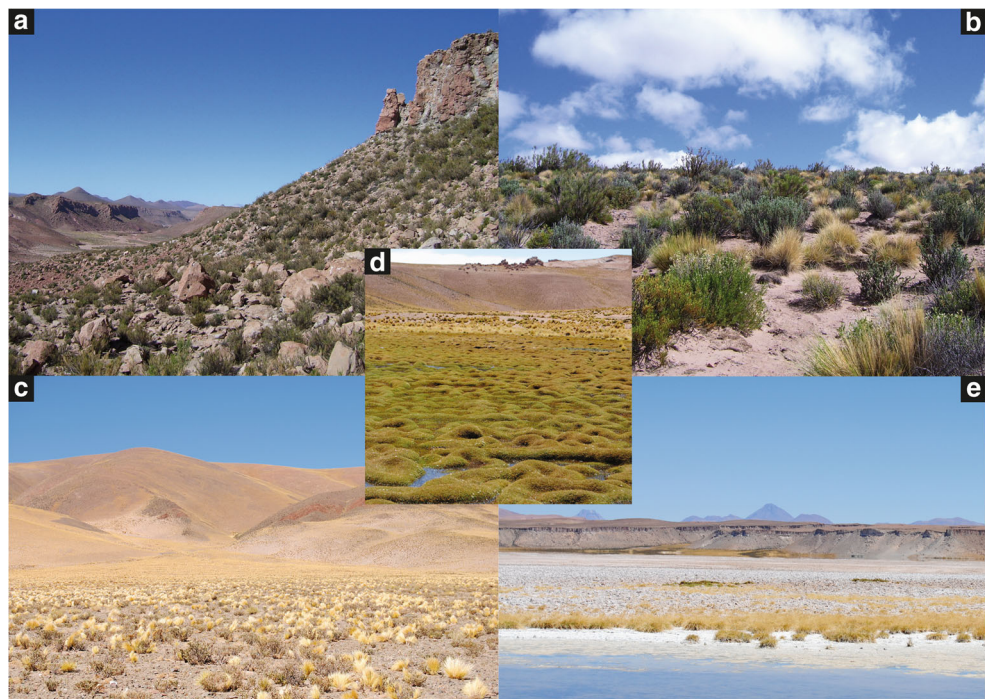
The study area: the dry Puna of Argentina

The Puna of Argentina is located between 22° and 27° S and between 3000 and 5000 masl. This region is a highland desert that contains several NE-SW oriented mountain ranges. It is characterised by wide temperature variation between day and night, high solar radiation and low atmospheric pressure due to altitude. The only sources of freshwater are a few rivers and several springs scattered throughout the landscape. Primary productivity is concentrated on stable hydrological systems such as primary basins, high ravines and wetlands. Precipitation occurs during summertime and is governed by the South American monsoon system (Zhou and Lau 1998). This system produces about 80 % of the annual rainfall between December and February (Vuille and Keimig 2004). Precipitation also exhibits a latitudinal gradient which delimits two sub-regions within the Puna of Argentina: the dry Puna, located north of 24° S, with a mean annual precipitation of 300 mm/year; and the salt Puna, located south of 24° S, with a mean annual precipitation that barely reaches 100 mm/year (Bianchi et al. 2005).

Some of the most important plant communities identified in the dry Puna are the following (Cabrera 1976; Ruthsatz and Movia 1975; Braun Wilke et al. 1999) (Fig. 1):

1. Shrub steppe (*tolar*) is located between 3500 and 3900 masl. It is dominated by species such as *Parastrephia lepidophylla* and *Fabiana densa* and exhibits a low proportion of herbs (5 %).

Fig. 1 Plant communities in the dry Puna of Argentina. **a** Shrub steppe. **b** Mixed steppe. **c** Herbaceous steppe. **d** Wetland. **e** Salt flat



- Mixed steppe is located between 3900 and 4100 masl. It represents an ecotonal landscape and is composed of both grasses and shrubs.
- Herbaceous steppe (*pajonal*) is located between 4100 and 4700 masl. It is dominated by *Festuca* spp. and other grasses, like *Poa* spp. and *Stipa* spp.
- Wetlands (*vegas*) are scattered along the landscape between 3500 and 4700 masl. These are restricted patches with high biomass and plant cover through the whole year, composed mainly of hygrophilous grasses such as *Deyeuxia* spp. and *Muhlenbergia* spp.
- Salt flats (*Salinas* or *salaras*) are also scattered along the landscape between 3400 and 4200 masl. These large salt bodies are surrounded by flat zones colonised by sparse halophytic plants such as *Atriplex* spp. and *Distichlis* spp.

Materials and methods

Sampling locations

Plant specimens were collected at eight sites distributed along an altitudinal gradient from 3415 to 4245 masl (Fig. 2). These eight sites represent the five different plant communities described above. Salinas Grandes (3415 masl) is located in a vast salt flat characterised by low vegetation density and diversity. Ojo de Agua (3650 masl) is located at a gorge characterised by the presence of shrub steppe vegetation represented by shrubs

and some grasses. Lapao is a locality where two different plant communities are present: the shrub steppe (3680 masl), characterised by the presence of shrubs and some herbs, and the wetland (3660 masl), characterised by the presence of grasses and herbs. Pista (3890 masl) is located at a small hill characterised by the presence of shrub steppe vegetation represented by shrubs, grasses and some cacti. Curque (4040 masl) is located at the mixed steppe where both shrubs and highland grasses are represented. Taire is a locality where two different plant communities are present: the mixed steppe (4105 masl), characterised by the presence of both shrubs and grasses, and the wetland (4015 masl), characterised by the presence of grasses and herbs. Laguna Ana represents a salt flat (4110 masl) with low vegetation density and diversity, surrounded by an herbaceous steppe (4135 masl) where only some scattered grasses and shrubs are present. Tuzgle represents a vast wetland (4230 masl), characterised by the presence of sedges, herbs and grasses, surrounded by an herbaceous steppe (4235 masl) that develops on the slope of the Tuzgle volcano in which grasses dominate the vegetation.

Plant material

We employed a quadrat sampling technique (25 m² squares in all cases, except in the cases of Lapao where a total of 62 m² were sampled, and Taire and Laguna

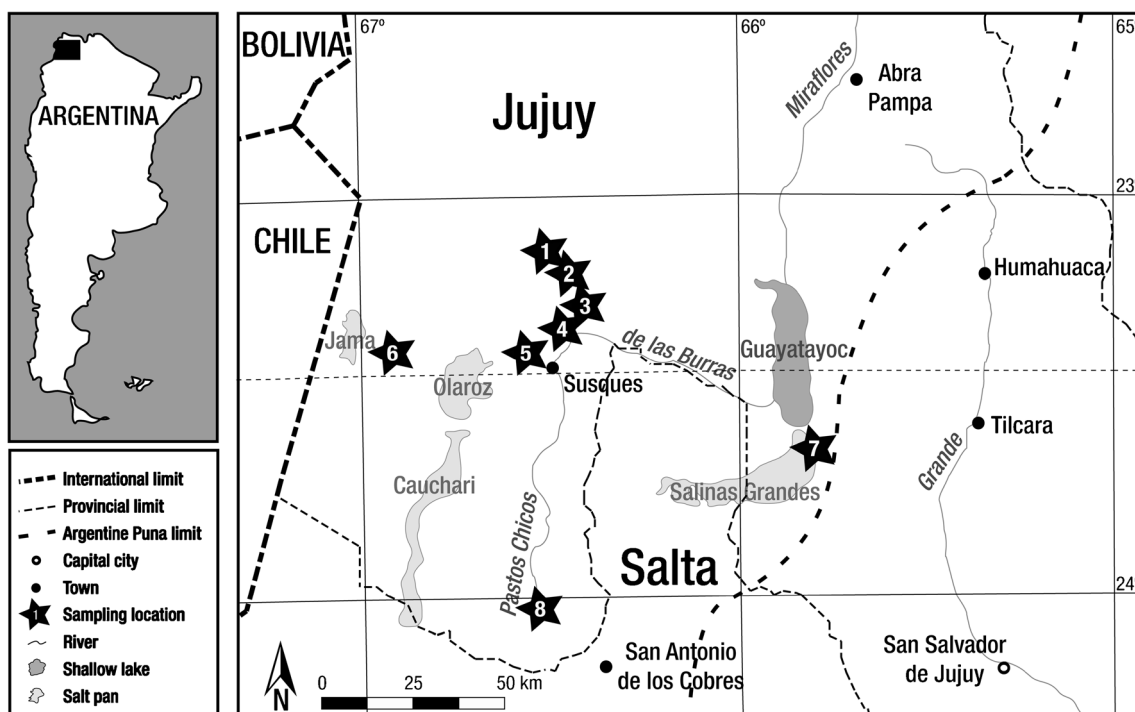


Fig. 2 Map displaying the sampling locations. 1 Curque, 2 Pista, 3 Lapao, 4 Ojo de Agua, 5 Taire, 6 Laguna Ana, 7 Salinas Grandes, and 8 Tuzgle

Ana where 8 m² were sampled) collecting at least a plant specimen for each species recognised in the field and more than one specimen in the case of the most represented species at each site. In this sense, taxa such as *Parastrephia* sp. (*tola*) which are not frequently ingested by SAC but are consistently represented in the vegetation assemblages were also collected. Once plant specimens were collected, they were pressed in brown paper bags and air-dried in the field.

The plants were identified to species in the field when possible, and if not in the laboratory, and then grouped into C₃ and C₄ photosynthetic pathways according to their $\delta^{13}\text{C}$ values, and compared to previous results for the area (Fernández et al. 1991; Fernández and Panarello 1999-2001; Panarello and Fernández 2002). However, not all of the plants in this study were identified to species level (see supplementary Table 1).

Sample preparation

At the laboratory, edible plant parts (mostly leaves and stems, see supplementary Table 1) were washed with ultrasonic baths for 45 min and then oven dried at 60 °C for 24 h. Afterwards, the samples were hand ground using an agate mortar and pestle and homogenised to obtain the average isotopic composition for each plant specimen (Cadwallader et al. 2012). We recognise that by selecting the edible parts of the plant specimens and homogenising them, our results may be masking some of the variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between different plant tissues (Badeck et al. 2005; Szpak 2014). Nevertheless, we consider that these variations do not represent a major problem in setting a paleodietary baseline because most of these differences are below 0.5 ‰ and do not exhibit a clear pattern (Szpak et al. 2013).

Mass spectrometry

Measurements of each sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were made on a CarloErba Elemental Analyser (CHONS) coupled to a Finnigan MAT Delta V continuous-flow isotope ratio mass spectrometer (CF-IRMS) through a Thermo ConFlo IV interface using internal standards. These standards (caffeine: $\delta^{13}\text{C}=-39.33$ ‰, $\delta^{15}\text{N}=7.02$ ‰; sugar: $\delta^{13}\text{C}=-11.41$ ‰; and collagen: $\delta^{13}\text{C}=-18.18$ ‰, $\delta^{15}\text{N}=6.12$ ‰) were calibrated against VPDB and AIR reference standards for carbon (L-SVEC, NBS-19 and NBS-22) and nitrogen (IAEA N1 and IAEA N2) (Coplen et al. 1992, 2006; Craig 1957). Replicates of internal standards showed analytical errors (SD) to be on the order of ± 0.2 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Results

We analysed a total of 150 plant specimens, which exhibited $\delta^{13}\text{C}$ values ranging from -31.7 to -12.2 ‰ and $\delta^{15}\text{N}$ values ranging from -3.1 to 13 ‰ (supplementary Table 1). For C₃ plant specimens ($n=131$), $\delta^{13}\text{C}$ values ranged from -31.7 to -21 ‰, with a mean value of -25.4 ‰, and $\delta^{15}\text{N}$ values ranged from -3.1 to 13 ‰, with a mean value of 3.7 ‰, reflecting in both cases a normal distribution (Shapiro-Wilk test for C₃ plants $\delta^{13}\text{C}$ values $W=0.98$, $p=0.10$ and $\delta^{15}\text{N}$ values $W=0.99$, $p=0.39$). For C₄ plant specimens ($n=16$), $\delta^{13}\text{C}$ values ranged from -15.7 to -12.2 ‰, with a mean value of -14.2 ‰, and $\delta^{15}\text{N}$ values ranged from 1.1 to 8.6 ‰, with a mean value of 4.8 ‰, reflecting in both cases a normal distribution (Shapiro-Wilk test for C₄ plants $\delta^{13}\text{C}$ values $W=0.95$, $p=0.56$ and $\delta^{15}\text{N}$ values $W=0.90$, $p=0.10$). For CAM plant specimens ($n=3$), $\delta^{13}\text{C}$ values ranged from -14.7 to -12.8 ‰, with a mean value of -13.8 ‰, and $\delta^{15}\text{N}$ values ranged from 4.5 to 6.0 ‰, with a mean value of 5.2 ‰. As can be observed, CAM plant carbon stable isotope composition falls within the C₄ range of $\delta^{13}\text{C}$ values, reflecting the arid conditions of the environment in which they grew (Eickmeier and Bender 1976). Of all the specimens sampled in this study, C₄ plant species are mostly grasses ($n=13$) while C₃ plant species are mostly shrubs ($n=61$), but there are also grasses ($n=34$) and some herbs ($n=31$), as expected in hot dry regions (Koch et al. 1991) (supplementary Table 1).

These results show that C₃ plants are by far the most abundant in all localities sampled regardless of altitude (Table 1). In turn, C₄ plants are present in five of the eight sampled localities and these five are located along the whole altitudinal gradient sampled, contrary as expected considering previous studies (Panarello and Fernández 2002; Samec 2014; Szpak et al. 2013; Tieszen and Chapman 1992). At Salinas Grandes and Taire mixed steppe sites, 33 % of the plant specimens sampled ($n=3$ specimens at both sites) were C₄ plants; whereas, at Lapao shrub steppe site, 14 % of the plant specimens sampled ($n=43$) were C₄ plants (Table 1). Thus, C₄ plants are present in all the vegetation communities sampled: shrub steppe, mixed steppe, herbaceous steppe, wetland and salt flat. However, if we compare localities sampled below and above 3900 masl, C₄ plants are more abundant below that threshold (C₄ plants <3900 masl: $n=12$, $\%=13.79$, including CAM plants: $n=15$, $\%=17.24$, vs. C₄ plants >3900 masl: $n=4$, $\%=6.35$), reflecting a differential distribution of these plants along the gradient, as expected from previous results (Panarello and Fernández 2002; Samec 2014; Szpak et al. 2013; Tieszen and Chapman 1992).

$\delta^{13}\text{C}$ values do not show a correlation with altitude ($r=-0.11$, $p=0.18$), but this is to be expected given that both C₃ and C₄ plants are being considered. Taking into account only C₃ plants, $\delta^{13}\text{C}$ values also do not show a significant correlation ($r=-0.05$, $p=0.56$), in contrary to results reported

Table 1 The number of plants sampled (C₃, C₄ and CAM) according to locality

Site	Plant community	Latitude S	Longitude O	Altitude masl	N plant specimens sampled	C ₃ plants sampled	% C ₃ plants	C ₄ plants sampled	% C ₄ plants	CAM plants sampled	% CAM plants
Salinas Grandes	Salt flat	23° 37' 04.00"	65° 51' 25.80"	3415	3	2	67	1	33	0	0
Ojo de Agua	Shrub steppe	23° 23' 05.50"	66° 22' 29.10"	3650	10	10	100	0	0	0	0
Lapao	Wetland	23° 21' 58.50"	66° 21' 63.50"	3660	18	16	89	2	11	0	0
	Shrub steppe	23° 21' 55.07"	66° 21' 52.91"	3680	43	36	84	6	14	1	2
Pista	Shrub steppe	23° 19' 49.27"	66° 24' 07.15"	3890	13	8	62	3	23	2	15
Curque	Mixed steppe	23° 15' 54.95"	66° 26' 21.60"	4040	22	22	100	0	0	0	0
Taire	Wetland	23° 24' 36.10"	66° 30' 16.60"	4015	6	5	83	1	17	0	0
	Mixed steppe	23° 24' 02.00"	66° 31' 31.90"	4105	3	2	67	1	33	0	0
Laguna Ana	Salt flat	23° 23' 56.47"	66° 57' 27.00"	4110	3	3	100	0	0	0	0
	Herbaceous steppe	23° 23' 56.47"	66° 57' 23.60"	4135	3	3	100	0	0	0	0
Tuzgle	Herbaceous steppe	24° 02' 10.01"	66° 31' 18.20"	4245	10	8	80	2	20	0	0
	Wetland	24° 02' 10.10"	66° 31' 23.00"	4230	16	16	100	0	0	0	0
Totals					150	131	87	16	11	3	2

in previous investigations, although the altitudinal range surveyed in these studies was wider (~0–4000 masl) than the one considered here (Körner et al. 1991; Szpak et al. 2013) (Fig. 3). On the other hand, $\delta^{15}\text{N}$ values of both C₃ and C₄ plants exhibit a significant negative correlation with altitude ($r=-0.64$, $p=5.6 \times 10^{-19}$) since values decrease as altitude increases, as expected based on previous investigations (Ambrose 1991; Szpak et al. 2013) (Fig. 4).

Discussion: implications for archaeological research

The study of the variation in plant isotopic compositions is particularly relevant as a baseline for the reconstruction of prehistoric diets of human and animal populations by means of isotopic analyses (Cadwallader et al. 2012; Casey and Post 2011; Szpak et al. 2013). Although most of the wild plants analysed in this study would not have been consumed directly by the human groups that occupied the dry Puna in the past, these results are important as a baseline for the reconstruction of prehistoric animal exploitation strategies and particularly herd management practices (Finucane et al. 2006; Thornton et al. 2011).

As expected from previous results for the area, our results show that C₃ plants are predominant in all the plant communities sampled and that the $\delta^{13}\text{C}$ values of both C₃ and C₄ plants overlap with those presented in previous works (Fernández et al. 1991; Panarello and Fernández 2002). At the same time, the $\delta^{15}\text{N}$ values of the sampled plants overlap with previous results from other arid areas, such as East and South Africa (Ambrose 1991; Heaton 1987).

Our results have identified differences in the relative abundances of C₃ and C₄ plants between the different vegetation

communities sampled; these present a distribution that would counteract the effects of atmospheric pressure differences marked by altitude over C₃ plant $\delta^{13}\text{C}$ values and therefore affect the average $\delta^{13}\text{C}$ signal for each plant community (Tieszen and Chapman 1992). In this sense, C₄ plants are proportionately more abundant at low altitude and dry sites in relation to high altitude and moister ones and, thus, the average $\delta^{13}\text{C}$ value of the natural pastures available along the altitudinal range considered will be higher at low-altitude sites (Szpak et al. 2013). Furthermore, our results do not show a positive correlation between altitude and C₃ plant $\delta^{13}\text{C}$ values as suggested by previous works, although the altitudinal range considered here is particularly narrow in comparison with those studies (~3400–4300 masl vs. ~0–4000 masl) (Körner et al. 1991; Szpak et al. 2013). It is important to mention that the differences in water availability between the sampling locations considered here are also a factor that could interfere with the expected pattern for C₃ plants, as exposed before (Tieszen and Chapman 1992). On the other hand, our results show that $\delta^{15}\text{N}$ values correlate with altitude as a response to differences in moisture availability between low- and high-altitude sites, as expected according to previous studies (Ambrose 1991; Szpak et al. 2013).

If we consider the patterns described here, altitude seems to be the most important variable affecting the distribution of C₃ and C₄ plants, and therefore the average $\delta^{13}\text{C}$ signal for each plant community, and also their $\delta^{15}\text{N}$ values. Nevertheless, we consider that altitude by itself does not explain the differential distribution of C₃ and C₄ plants or the distribution of the $\delta^{15}\text{N}$ values; instead, water availability and temperature determined by altitude seem to be the causal factors for this pattern. Unfortunately, this is only a working hypothesis that cannot be addressed by this study since there are no measured climate

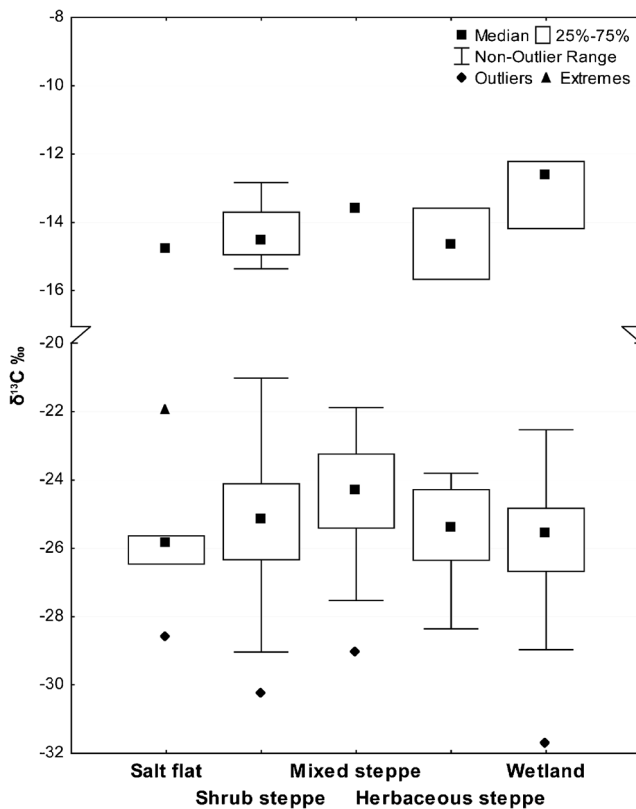


Fig. 3 Carbon isotopic composition ($\delta^{13}\text{C}$) of sampled plants according to vegetation communities

data for some of the localities sampled due to the scattered distribution of climate stations in the Puna of Argentina.

At this point, our results confirm that the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on SAC from low-altitude sites compared with the lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on SAC from high-altitude sites within the dry Puna of Argentina already published in previous studies can be explained by the consumption of local plants (Fernández and Panarello

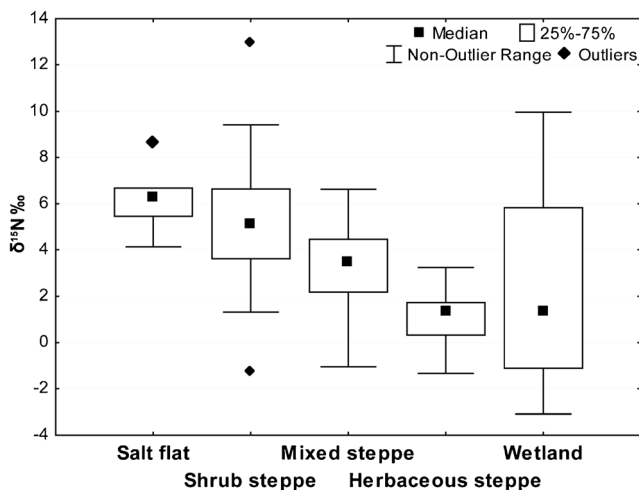


Fig. 4 Nitrogen isotopic composition ($\delta^{15}\text{N}$) of sampled plants according to vegetation communities

1999–2001; Samec 2012, 2014; Yacobaccio et al. 2009). In this sense, previous analyses performed on bone collagen extracted from both wild and domesticated modern SAC resulted in a significant correlation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with altitude (Samec 2012, 2014; Samec et al. 2014; Yacobaccio et al. 2009) in accordance with other results within the Andean area (Thornton et al. 2011). In a previous work, Samec (2014) explored the diet of two contemporary llama herds which were fed natural pastures from different plant communities. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the two herds showed significant differences; the herd feeding below 3900 masl presented a mean $\delta^{13}\text{C}$ value of -17.6 ‰ and a mean $\delta^{15}\text{N}$ value of 8.3 ‰; whereas, the herd feeding above 3900 masl presented a mean $\delta^{13}\text{C}$ value of -19.6 ‰ and a mean $\delta^{15}\text{N}$ value of 5.9 ‰. At the same time, Samec (2014) estimated 95 % confidence intervals for the percentage of C_4 and CAM plants included in the diet of both herds using the model of Phillips and Gregg (2001). These resulted in a range between 19 and 27 % in the case of the herd feeding below the 3900 masl threshold and a range between 0 and 9 % in the case of the herd feeding above that threshold, approaching the percentages of C_4 and CAM plants present in the plant communities sampled above and below 3900 masl and presented in this study. Thus, previous results measured on modern llama bone collagen now can be easily explained by the natural abundances of C_3 and C_4 plants and the distribution of their $\delta^{15}\text{N}$ values along the altitudinal range sampled within this study. These results can be employed to distinguish the use of plant communities placed below 3900 and above 3900 masl as pasturelands by the pastoral groups that occupied this area in the past by comparing these modern standards with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on archaeological bone materials. In the future, we hope to be able to establish the seasonal use of the different plant communities considered here by performing a serial sampling of llama tooth tissues.

Final remarks

The application of stable isotope analyses to the study of human diets in the past has a long history in archaeology (Hastorf 1985; Tykot 2004). Along its development, the need for isotopic baselines for accurate interpretations has become evident to most archaeologists employing these techniques. Nevertheless, most of the attempts to develop isotopic baselines for dietary reconstruction have focused on vertebrate fauna (Katzenberg and Weber 1999; Müldner and Richards 2005; Richards et al. 2000, among many others). This study moves a step forward by providing a better understanding of the baseline isotopic variation in plants from the dry Puna of Argentina, putting the emphasis in the sampling of natural pastures employed by the modern pastoral groups that inhabit the area. These groups employ traditional herding strategies

that often involve the use of different pasturelands located in different plant communities at different altitudes during the annual cycle (Yacobaccio 2007). Yacobaccio et al. (1998) have found that the herders of the Susques area within the dry Puna of Argentina employ grass steppes and mixed steppes as winter pastures during the dry season, and shrub steppes and wetlands as summer pastures during the wet season. Keeping this information in mind, the development of an isotopic ecology for the area could provide a new tool to explore questions such as herders' mobility and pastureland use in the past by means of isotopic analysis of animal tissues. In this sense, the isotopic compositions measured on archaeofaunal remains could be interpreted through the frame of reference composed of modern plant and herbivore isotopic values (Ambrose 1991). In the study area, previous investigations had already employed modern SAC values to interpret carbon and nitrogen isotopic compositions of SAC remains recovered in pastoral sites with remarkable results (see Fernández and Panarello 1999–2001; Yacobaccio et al. 2010). In this sense, the results presented here will provide a full picture on that matter, allowing us to explain variation in the isotopic composition of animal tissues through variation in the isotopic composition of the plants consumed and its relation to environmental variables determined by altitude such as temperature and water availability.

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