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ORIGINAL PAPER

Dietary patterns in human populations from northwest Patagonia during Holocene: an approach using Binford's frames of reference and Bayesian isotope mixing models

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Abstract The goal of this paper is to assess the variation in the proportional contribution of diverse resources to the diet of human populations from northwest Patagonia (Argentina) throughout the Middle-Late Holocene. Particularly, we assessed the variation among three geographic areas and two periods. We first estimated the expected proportions of terrestrial animals and plants and aquatic resources for each area according to the Binford's frames of references approach. A Bayesian mixing method was then applied to calculate the proportion of plants and animals in the diets from stable isotopes (δ^{13}C and δ^{15}N) of human bone collagen. The isotope values suggest that the composition of diets differed spatially and temporally. Diets of South Mendoza were mainly composed of terrestrial animals (*Rhea-Lama* and rodents) with a greater incorporation of C_3 plants towards the later Late Holocene; in North Neuquén, *Rhea* and *Lama* represent a proportion of 0.84 of the diet consumed; and finally, the sample of Center Neuquén is the only one with high values of *Araucaria* in the diet. The isotopic values obtained for the three studied areas did not fit to the expectations of Binford's model, North Neuquén being the area that departs most from the predicted proportions of terrestrial animals and plants and aquatic organisms in the diet. These findings open up new questions about the local conditions that influenced regional variation in the diet of prehistoric hunter-gatherers.

Keywords Patagonia · Diet · MixSIAR · EnvCalc · δ^{13}C · δ^{15}N

Introduction

The study of variation in the diet of human populations that inhabited Patagonian region during the Holocene has been the focus of archeological and bioanthropological research in the last 15 years (Barberena 2002; Borrero et al. 2009; Favier Dubois et al. 2009; Gómez Otero 2007; Gordón et al. 2015; Martínez et al. 2009; Moreno et al. 2011; Tessone 2010). On the basis of isotope data from human bones analyzed by means of qualitative and quantitative univariate techniques, a coarse grain pattern of variation across Patagonia has been established. Overall, this pattern is characterized by the consumption of terrestrial animals in populations inhabiting the steppe (mainly *Lama guanicoe*), diets that included marine resources in the coast, and finally, diets with a significant contribution of plants in the Andean forest of North Patagonia (Favier Dubois et al. 2009; Fernández 1988–1990; Fernández and Tessone 2014; Gómez Otero et al. 2015; Panarello et al. 2006; Tessone et al. 2009). Even though the broad properties of diets of Patagonian hunter-gatherers are relatively well established, for some areas such as northwest Patagonia, the information is still scarce or lacking.

Northwest Patagonia has been inhabited by humans since the Pleistocene-Holocene transition. In the initial peopling,

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around 12,000 calibrated years before present (cal. BP), the population size was relatively small, then increased between 7000 and 5000 years ago, and reached a maximum size around 1000 years ago (Perez et al. 2016). Throughout the Holocene, this area displayed high levels of environmental heterogeneity with great availability of resources even at restricted geographical scales (Barberena 2013; Hajduk et al. 2007; Navarro et al. 2012). Based on zooarcheological and archeobotanical evidence, it has been hypothesized that human groups from this area mainly incorporated into their diet wild plants such as *Prosopis* sp., *Araucaria araucana*, and *Geoffroea decorticans* (Fernández 1988–1990; Lema et al. 2012; Llano 2015) and herbivores such as *L guanicoe*, *Rhea pennata*, *Lagostomus maximus*, *Lagidium viscacia*, and *Ctenomys* sp. (Barberena et al. 2015; Borrero 2005; Fernández 1988–1990; Giardina 2012). The consumption of other resources such as birds, freshwater organisms, and *Zea mays* has also been suggested, although they may not have had a significant contribution to the diets (Fernández 1988–1990; Gil 2003; Novellino et al. 2004; Giardina et al. 2014).

Despite the fact that the animal and plant resources potentially consumed by prehistoric human populations from northwest Patagonia have been identified in the archeological record, the proportion in which they were incorporated into the diet remains unknown. Assessing relative contributions of different sources to the diet of hunter-gatherers is relevant to explore subtle variations in subsistence strategies among groups that might be related to demographic and ecological processes (Johnson 2014). This requires the use of quantitative models that allow a formal generation and testing of hypotheses. A promising avenue in this sense is the conjoint use of models based on environmental information—e.g., latitude, temperature, precipitation, and distance to the sea—and ethnographic data to derive expectations about the subsistence dependence on different resources of hunter-gatherers (Binford 2001; Johnson 2014; Johnson et al. 2015), along with stable isotopes analyzed by means of Bayesian mixing models (Moore and Semmens 2008; Parnell et al. 2013; Semmens et al. 2009). The two approaches are specifically related since the first one generates expectations in terms of the proportion in the diet of terrestrial animals and plants and aquatic organisms, while the Bayesian mixing models provide a probabilistic estimation of the relative contribution of different resources to the diets of consumers.

The aim of this work is to estimate variation in the proportional contribution of diverse resources to the diet of human populations across northwest Patagonia (between 35° and 39° south latitude) during the Middle-Late Holocene (6000–200 cal. BP). We particularly assessed geographical variation among three areas—South Mendoza, North Neuquén, and Center Neuquén—delimited from north to south on the basis of archeological and environmental data. We first estimated the expected subsistence dependence on hunting and

gathering and on aquatic resources in the human groups from our region of study based on the approach developed by Binford (2001) and Johnson (2014). These estimations offer a baseline for comparing with the proportion of plants and animals in the diets calculated on the basis of stable isotopes (δ^{13}C and δ^{15}N) from human bone collagen analyzed by a Bayesian mixing model (Moore and Semmens 2008; Parnell et al. 2013; Semmens et al. 2009). The results obtained are discussed in the context of technological, zooarcheological, and archeobotanical information; demographic estimations; and bioanthropological diet indicators available for the region.

Materials and methods

Analysis of dietary expectations based on environmental parameters

With the purpose of generating expected values of subsistence dependence on hunting and gathering and on aquatic resources for the hunter-gatherers from northwest Patagonia, we applied the approach developed by Binford (2001) and Johnson (2014). On the basis of ethnographic data of most of the documented contemporary hunter-gatherers and environmental information, Binford (2001, p. 118) found that subsistence strategies are related to the effective temperature (ET) and population density. In this model, subsistence refers specifically to dietary dependence expressed as the percentage of total diet derived from terrestrial animals and plants and aquatic organisms (Binford 2001; Johnson 2002). These estimations are based on ethnographic descriptions of subsistence activities and the composition of typical meals (Johnson personal communication). At high latitudes (ET ≤ 12.75 °C), low-population-density hunter-gatherers are primarily dependent on hunting terrestrial animals. As the latitude decreases, and consequently the ET is higher, hunter-gatherers are often primarily dependent on plant foods. Population density can increase beyond a packing threshold of 9.1 persons/100 km² only when intensification strategies are developed. Binford (2001, p. 363) defines intensification as "the process that impels hunter gatherers to increase the amount of food they extract from smaller and smaller segments of the landscape". Intensification options vary according to the ET and the availability of aquatic resources: for settings at high latitudes, where aquatic resources are abundant, hunter-gatherer dependence on them increases as population density increases; for setting with middle ranges of ET (12.75–15.25 °C), where aquatic resources are not an intensification option (proportion of fishing <0.30), terrestrial plants are the only intensification option. These generalizations based on empiric evidence are used as a frame of reference to predict past patterns of variation at particular regional settings, which can be then compared with archeological data (Binford 2001; Johnson 2014).

On the basis of climatic variables, the model allows us to derive expectations about the dietary dependence on terrestrial animals and plants and aquatic organisms, as well as demographic density for a given environmental setting. In order to obtain these estimations, we collected current climatic data from weather station records for three cities from northwest Patagonia: Malargüe (South Mendoza), Chos Malal (North Neuquén), and Las Lajas (Center Neuquén) (Fig. 1). For Malargüe city, we used temperature and precipitation records between 1981 and 1990 available through the national weather service (Malargüe 2016). For Chos Malal city, the information available corresponds to the period 1901–1960 (Datos meteorológicos y pluviométricos 2016). Values of precipitation for Las Lajas city were obtained for the periods 1901–1970, while the records of temperature were only available for the first period (Datos meteorológicos y pluviométricos1 2016). From these data, we estimated the effective temperature as ET = [(18 × MWM) − (10 × MCM)] / [(MWM − MCM) + 8], where MWM is the mean temperature for the warmest month and MCM is the mean temperature for the coldest month of the year (Binford 2001, p. 59). Additionally, we estimated the elevation above the sea level, the distance to the sea, type of soil, and vegetation. These variables were obtained from maps generated by the National Institute of Agricultural Technology (Cruzate 2011a, b). Dietary and demographic expectations were generated by using the Environmental Calculations program— EnvCalc 2.1 (Binford and Johnson 2006). We calculated the expected dependence on terrestrial animals and plants (WHUNTP and WGATHP, respectively) and aquatic organisms (WFISHP). It is important to take into account that the lack of anadromous fish in south hemisphere makes projections based on cases from the north hemisphere problematic because they overestimate the dependence on fishing (Binford 2008). This model also provides an estimation of population density per 100 km^2 as the amount of people that can be supported by easily accessible terrestrial resources without culture aids mediating the access to resources (TERMD2). Such measure is used as a baseline population density for hunter-gatherers in a given environmental setting (Binford 2001, p. 187). In addition, the projected density for populations like known hunter-gatherers in similar environmental settings was estimated (WDEN).

Analytical procedures for the determination of stable isotopes

To study the stable isotopes (δ^{13}C and δ^{15}N) of human samples, we selected bone remains from 24 individuals recovered from archeological sites from Neuquén (Table 1). The analysis of human bones was conducted under the ethical guidelines of the Asociación Argentina de Antropología Biológica and federal and provincial laws for the protection of archeological patrimony (Laws 25,743, and 2184). Only adults were included in this study because younger individuals tend to display greater variation in their isotopes as a consequence of the enrichment in ^{15}N that takes place when the diet incorporates breast milk (Fogel et al. 1989; Waters-Rist and Katzenberg 2010). Individuals were considered adults on the basis of the obliteration of the sphenobasilar suture and eruption of the third molar (Buikstra and Ubelaker 1994). Sex was estimated using cranial and pelvic traits (Buikstra and Ubelaker 1994). Whenever possible, the ribs were processed for these analyses; otherwise, the study was done using carpal and tarsal bones. These bones with low density have a faster turnover rate than more dense bones (Pfeiffer et al. 2006), and thus, their isotopic signal can be taken as a better proxy of adult diets. Additionally, samples of faunal remains were analyzed including specimens of *R. pennata* (*n* = 1), *Equus caballus* (*n* = 1), *Ctenomys* sp. (*n* = 1), and ovicaprids (*n* = 1) (Supplementary Table S1). In these analyses, the ribs were also prioritized over other bones.
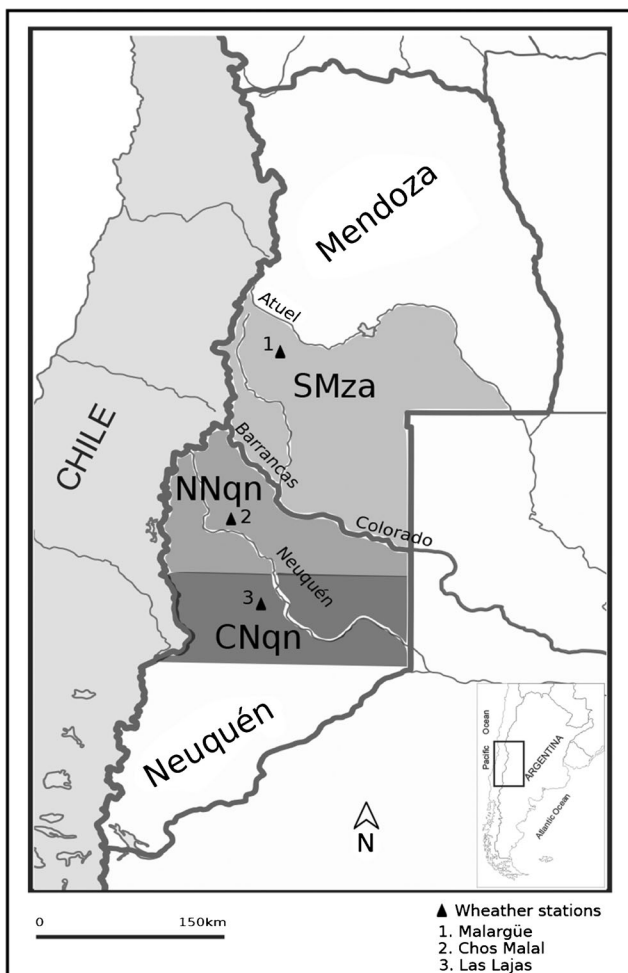

Fig. 1 Map of northwest Patagonia showing the three geographic areas studied: South Mendoza (*SMza*), North Neuquén (*NNqn*), and Center Neuquén (*CNqn*)

Table 1 Stable isotope values (δ^{13}C and δ^{15}N) of human samples from northwest Patagonia obtained in this work

Population	Site	Individual	Sex	δ13C	%C	δ15N	%N	C:N
NNqn1	Gubevi		I	−18.5	41.9	7.0	13.8	3.5
NNqn1	Hermanos Lazcano	Ent5 C1A	F	−18.6	40.7	6.9	14.2	3.3
NNqn1	Hermanos Lazcano	C2 I1	M	−18.5	41.5	6.7	14.5	3.3
NNqn1	Hermanos Lazcano	II 3.3	F	−18.4	39.6	7.3	13.6	3.4
NNqn1	Aquihuecó	19.1	F	−18.2	39.3	7.5	13.8	3.3
NNqn1	Aquihuecó	38	M	−17.9	41.6	9.9	14.9	3.3
NNqn1	Aquihuecó	16	F	−17.6	42.6	7.5	15.2	3.3
NNqn1	Aquihuecó	31	F	−18.1	41.5	7.3	14.9	3.3
NNqn1	Aquihuecó	30	M	−17.9	40.3	10.0	14.4	3.3
NNqn1	Aquihuecó	23	M	−17.9	39.3	10.2	14.2	3.2
NNqn1	Aquihuecó	19.2	F	−18.0	38.9	8.2	13.8	3.3
NNqn1	Aquihuecó	27	M	−18.0	[a]	8.7	[a]	3.2
NNqn1	Aquihuecó	33	M	−18.4	[a]	7.1	[a]	3.3
NNqn1	Aquihuecó	34	M	−18.3	[a]	10.4	[a]	3.2
NNqn1	Aquihuecó	40	M	−18.3	[a]	8.5	[a]	3.2
NNqn2	Andacollo		M	−18.7	44.0	9.9	15.8	3.3
NNqn2	Caepe Malal	12 E2	M	−18.7	40.3	9.7	14.3	3.2
NNqn2	Caepe Malal	E7	I	−18.6	39.7	10.3	14.0	3.3
NNqn2	Caepe Malal	E1 C2	M	−18.4	37.9	9.9	13.5	3.3
NNqn2	Caepe Malal	Cr26	I	−19.0	37.0	10.6	12.3	3.5
NNqn2	Caepe Malal	E8	F	−18.9	41.6	10.1	14.2	3.4
NNqn2	Caepe Malal	Cr40	I	−18.1	38.7	11.6	12.9	3.5
NNqn2	Caepe Malal	E4	F	−18.7	41.1	9.5	14.6	3.3
CNqn1	Michacheo		F	−18.4	41.9	8.1	15.0	3.3

[a] Data not reported by the laboratory

The extraction of collagen was performed in the laboratories of the Institute of Isotopic Geology and Geochronology (INGEIS, Buenos Aires, Argentina). In order to separate the collagen fraction from the mineral fraction of the bone, a standard procedure was followed to clean and grind each sample. Briefly, the bones were first cleaned using abrasive techniques and ultrasonically washed. Then, the samples were demineralized by soaking them in a solution of 2% HCl for 72 h. In order to eliminate other postdepositional organic phases introduced during the burial process, the samples were further treated with NaOH 0.1 M during 24 h before and after the osseous demineralization. Finally, the samples were dried at 60 °C (Tykot 2004).

The estimation of the stable isotope abundance ratios (^{13}C/^{12}C and ^{15}N/^{14}N) was done with a Carlo Erba EA1108 Elemental Analyzer (CHN), connected to a continuous flow Thermo Scientific Delta V Advantage mass spectrometer through a Thermo Scientific ConFlo IV interface. These abundance ratios were determined relative to the ratios of those same isotopes in standard materials. Results are expressed as the difference (δ value) per mil (‰) between the ratio of isotopes (^{13}C/^{12}C or ^{15}N/^{14}N) in the sample and the standard, by using the Vienna Pee Dee Belemnite (VPDB) standard and Air, respectively. The ratio C/N was taken into account to assess the quality of the collagen in relation to possible sources of contamination (van Klinken 1999). The precision of the measurements was ±0.2‰ for both isotopes.

Database of stable isotopes of human remains and resources

A database of isotopic values of δ^{13}C and δ^{15}N from bone collagen of 55 adult individuals of both sexes was built by incorporating the isotopes of 31 individuals from previous studies (see Supplementary Table S2; Fernández and Panarello 2001; Gil et al. 2011; Salgán et al. 2012). This database includes specimens of archeological sites from South Mendoza and Neuquén, located between 35° to 39° south latitude (Fig. 1). No differences between males and females were found, and thus, data from both sexes were analyzed together. These individuals were grouped in samples corresponding to three geographical areas: South Mendoza (SMza—the area between Atuel river and Barrancas-Colorado river), North Neuquén (NNqn—the area between

Barrancas-Colorado river and the 38th parallel south), and Center Neuquén (CNqn—the area between the 38th and 39th parallels south) (Fig. 1). The samples were further separated into two periods: older than 1750 cal. BP (SMza1, NNqn1, and CNqn) and 1750–200 cal. BP (SMza2 and NNqn2). These periods were defined on the basis of archeological evidence that suggests dietary changes around that date—e.g. use of pottery and increased frequency of dental caries in human remains—(Della Negra 2008; Fernández 1988–1990; Gordón and Novellino 2016; Kozameh and Barbosa 1988–1990; Lema et al. 2012; Neme 2007).

With the aim of establishing the contribution of different resources to the diet of the human populations under study, we built an isotope ecology using 113 values of $\delta^{13}C$ and $\delta^{15}N$ taken from published databases (Boeckx et al. 2005; Fernández et al. 2016; Giardina et al. 2014; Gil et al. 2006, 2009, 2011, 2016; Quiroga et al. 2016; Rivas et al. 2012) and from this work (Supplementary Tables S1 and S3). This information corresponds to archeological and modern plants and animals from Neuquén and South Mendoza. Only for *A. araucana* and *Z. mays* (corn), we used values obtained from neighbor areas (Central Chile, North Mendoza, and San Juan) due to the lack of information for this resource in the region under study. The available resources were grouped in seven categories: (1) *Lama* and *Rhea* (*L. guanicoe* and *R. pennata*), (2) rodents (*Ctenomys* and *Lagostomus*), (3) C_3 plants (*Lagenaria*, *Cucurbitaceae*, *Geoffroea*, *Prosopis*, *Phaseolus*, and *Condalia*), (4) *Araucaria* (*A. araucana*), (5) Fish (*Perichthys* sp.), (6) birds (*Coscoroba coscoroba*, *Eudromia elegans*, and *Phoenicopterus chilensis*), and (7) corn (*Z. mays*). On the basis of the recommendations by Phillips et al. (2014), we set a maximum of seven types of resources because discriminatory power of mixing models declines when more resources are included. The categories were established on the basis of two criteria: first, previous archeological evidence suggests their contribution to prehistoric diets in the area under study; second, species within each group exhibit similar isotopic signatures. The mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values for each group of resources are shown in Supplementary Table S4. We further assessed the differentiation among the groups of resources by using a classical discriminant analysis, which indicates that the two isotopes have a discrimination power of 89% among resources.

Bayesian lineal mixing models

We applied a Bayesian mixing model to analyze the $\delta^{13}C$ and $\delta^{15}N$ values of consumers and resources. This model that extends the Bayesian models to multivariate data was used to estimate the proportional contribution of food resources to the human diets of populations from Neuquén and South Mendoza. It is important to remark that $\delta^{13}C$ from collagen reflects carbon contributions from protein (~75%) and carbohydrates plus lipids (~25%; Fernandes et al. 2012). The Bayesian mixing model incorporates uncertainty associated with multiple resources, fractionation values, and isotope signatures (Parnell et al. 2013; Stock and Semmens 2013). The analyses were carried out using the Bayesian method for stable isotope mixing models implemented in MixSIAR GUI for R (Stock and Semmens 2013). This method uses Markov chain Monte Carlo (MCMC) algorithms to generate a posterior probability distribution of the statistic of interest, which in our case is the diet proportion. We set populations and individuals as random effects and used the default parameters for MCMC, which correspond to the "very long" option. This option uses three parallel chains, with a MCMC for each chain of 1,000,000 iterations (attaining a total of 3,000,000 iterations). In order to avoid the autocorrelation in estimated values, the algorithm applies a sampling frequency of 300 iterations, obtaining a total of 10,000 estimations. The first 2300 estimations (corresponding to the first 700,000 iterations) were removed as burn-in (Stock and Semmens 2013). We determined the MCMC convergence of the posterior distributions for all variables using the trace plots and the Gelman-Rubin and Geweke diagnostic tests.

Paleodietary reconstructions are highly influenced by the isotope fractionation values used for $\delta^{13}C$ and $\delta^{15}N$. In a previous study, Bernal et al. (2016) showed that a combination of specific fractionations for different sources (Bocherens and Drucker 2003; Froehle et al. 2010; Hare et al. 1991; Tykot et al. 2009) produced better results than using a single value for all sources because it incorporates uncertainty and variation in trophic fractionation and isotopic values, which is inherent to natural systems. The estimations were based on the following fractionation values: $\Delta^{13}C$ $1.0 \pm 0.3/\Delta^{15}N$ 4.0 ± 1.0 for animals; $\Delta^{13}C$ $3.9 \pm 1.4/\Delta^{15}N$ 2.2 ± 0.3 for C_3 plants and *Araucaria*; and $\Delta^{13}C$ $3.7 \pm 1.4/\Delta^{15}N$ 2.3 ± 0.3 for corn. The value of 1.0‰ of $\Delta^{13}C$ for animals was calculated by Bocherens and Drucker (2003) on the basis of their estimations for bone collagen of different predators and their potential preys. Because collagen represents the average composition of diets at long term, the difference between the isotopic composition of collagen of predators and their preys reflects the enrichment associated to the increase in trophic level. The enrichment values for C_3 and C_4 plants were reported by Hare et al. (1991) from experimental studies. These authors found that total collagen from pigs grown on C_3 diets was enriched by 3.2‰ in $\Delta^{13}C$ and by 2.2‰ in $\Delta^{15}N$, while the collagen from pigs reared on C_4 diets was enriched by 1.4‰ in $\Delta^{13}C$ and by 2.3‰ in $\Delta^{15}N$. Modern samples were also corrected for the Suess effect by adding +1‰ to the $\delta^{13}C$ of the values of modern resources (Katzenberg et al. 2012).

Finally, the diversity in the proportion of resources within each group was evaluated using the Shannon H

diversity index, which measures the abundance and evenness of resources in the diet of consumers. The index $H = -\sum_{j=1}^{r} p_j \ln p_j$, where p_j is the proportion of the resource (r) j relative to the total resources.

Results

Table 2 shows the expected contribution of terrestrial animals and plants and aquatic organisms based on the effective temperature in the different geographic areas studied here. The climatic information obtained for Malargüe city suggests that similar proportions of terrestrial animals ($\simeq 0.30$) and plants ($\simeq 0.35$) and aquatic organisms ($\simeq 0.35$) are expected for populations from South Mendoza. These proportions are slightly different from those estimated for North and Center Neuquén with climatic data from Chos Malal and Las Lajas: terrestrial animals ($\simeq 0.35$) and plants ($\simeq 0.40$) and aquatic organisms ($\simeq 0.25$). The baseline population density (TERMD2) ranges from 1 to 1.2 individuals/100 km^2 in the three areas analyzed, while the population density expected for hunter-gatherers in similar settings (WDEN) was between 8.01 and 12.52 individuals/100 km^2 (Table 2).

The isospace of $\delta^{13}C$ and $\delta^{15}N$ shows that the early sample from South Mendoza (SMza1) is between the values of *Rhea-Lama*, rodents, and birds, while the later sample (SMza2) is close to the mean of the values of *Rhea-Lama*, rodents, C$_3$ plants, and birds (Fig. 2). The early sample from North Neuquén (NNqn1) is close to the values of *Rhea-Lama* and rodents, while the later sample from this area (NNqn2) is close to *Rhea-Lama* values. The sample from Center Neuquén is in between the values of rodents and *Araucaria* (Fig. 2).

The estimation of the proportional contribution of each type of resource to the diet obtained from $\delta^{13}C$ and $\delta^{15}N$ isotopes is shown in Table 3. For the earlier period from South Mendoza, the diet is mainly composed of *Rhea-Lama* (0.29) and rodents (0.20), with a contribution of around 0.10 of the other resources (except corn and fish that have a negligible contribution). In the later period, the proportion of C$_3$ plants increases (0.40), while the contributions of the other resources decrease. Distributions of posterior probabilities are shown in Supplementary Fig. S1.

In the case of the early sample from North Neuquén, the diet is composed of a large proportion of *Rhea-Lama* (0.58) with a lower proportion of *Araucaria* and rodents (around 0.16, Table 3). In the later period from North Neuquén (NNqn2), the diet is mostly composed of *Rhea-Lama* (0.77) followed by C$_3$ plants (0.12), while the proportion of other resources represents less than 0.10 of the diet. For the sample from Center Neuquén, the posterior probabilities indicate a high contribution of *Araucaria* (0.57) and rodents (0.23) to the diet, while the other sources only account for less than 0.10 of the diet (Table 3, Supplementary Fig. S1).

Overall, these results suggest that the composition of diets differs spatially, with the samples from South Mendoza displaying the highest values of Shannon H diversity index (Table 3). To explore the spatial patterns in more detail, the previous analyses were repeated grouping the individuals in the three areas without discriminating them by chronology. This analysis confirms the remarkable variation in diet composition among the three regions. In South Mendoza, diets are mainly composed of *Rhea-Lama* (0.35), C$_3$ plants (0.24), and rodents and birds (0.15). In North Neuquén, *Rhea-Lama* represents 0.84 of the diet, while in Center Neuquén, the diet is mainly composed of rodents (0.46) and *Araucaria* (0.41) (Supplementary Fig. S2 and Supplementary Table S5).

The correlation between the posterior probabilities of the seven groups of resources, which allows to determine whether or not it is possible to distinguish the specific contribution of each resource to the diet of consumers, is displayed in the Supplementary Fig. S3. Our results show very low negative correlations between pairs of resources, indicating that the relative contribution of each resource can be accurately ascertained.

Discussion

In this work, we employed a quantitative approach, which combines the generation of model-derived expectations about the proportion of resources consumed with the proportions estimated based on isotopic data from human remains, to explore the spatial and temporal patterns of variation of human

Table 2 Expected proportions of terrestrial animals and plants and aquatic resources and estimations of population densities (persons per 100 km^2) based on the effective temperature (°C) of the geographic areas studied

City	Effective temperature	Proportion of terrestrial animals	Proportion of terrestrial plants	Proportion of aquatic organisms	Baseline population density	Population density
Malargue	13.173	0.315	0.337	0.348	1.199	9.768
Chos Malal	13.897	0.345	0.425	0.231	1.105	8.010
Las Lajas	13.424	0.329	0.414	0.257	1.035	12.52

WHUNTP proportion of terrestrial animals, *WGATHP* proportion of terrestrial plants, *WFISHP* proportion of aquatic organisms, *TERMD2* baseline population density, *WDEN* population density

Fig. 2 Isospace plot of $\delta^{13}C$ and $\delta^{15}N$ for the resources and consumers grouped by a geographic area and time period
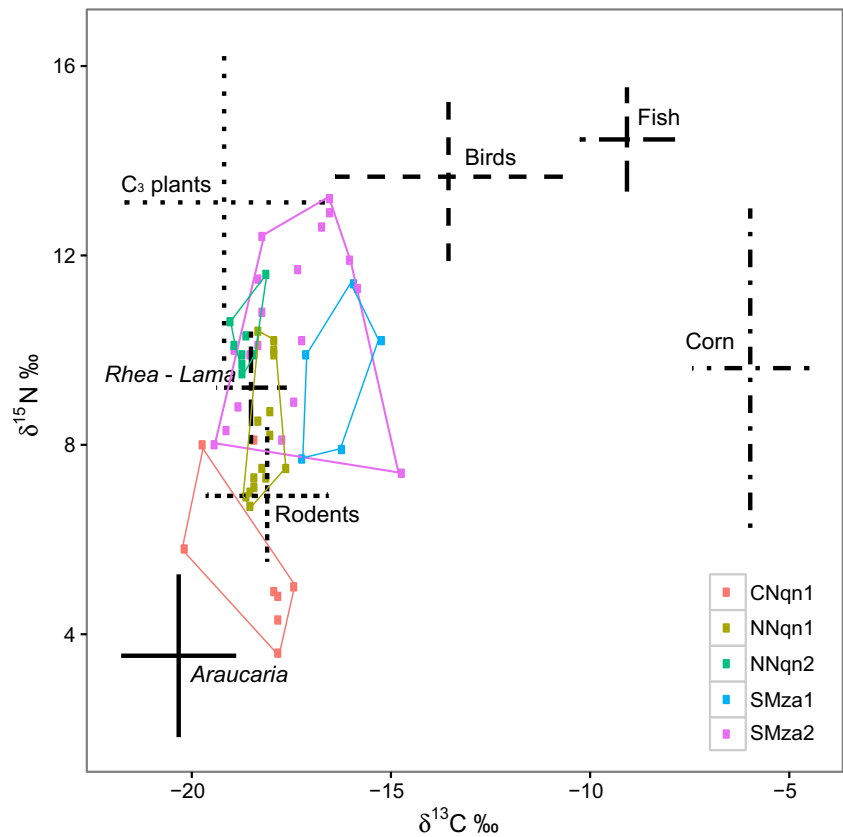
diets across different areas of northwest Patagonia. The model developed by Binford (2001) and Johnson (2002) provides rough estimations of the dietary dependence that are not intended to represent a precise picture of the past; rather, they are used as hypotheses of what would be expected for a given environmental setting on the basis of what is known for contemporary hunter-gatherers. Particularly for the areas under study, the model predicts that the diets of hunter-gatherers are expected to incorporate a similar proportion of terrestrial animals and plants and an important amount of aquatic organisms in South Mendoza, while in Neuquén, the aquatic resources were not an intensification option. These expectations were compared with the proportion of resources estimated by

a Bayesian mixed model using $\delta^{13}C$ and $\delta^{15}N$ of human bone collagen. The proportions derived from these $\delta^{13}C$ values were taken here as a measure of overall diet composition given that for the region of study, we previously demonstrated that apatite and collagen isotopes yield to similar dietary reconstructions, suggesting a similar contribution from protein and nonprotein dietary sources to the diet (Bernal et al. 2016). We found that the dietary dependence calculated from isotopic values did not fit to the expectations of the Binford's model in any of the three geographic areas studied, being North Neuquén the area that departs the most from the predicted proportions of terrestrial animals and plants and aquatic organisms in the diet.

Table 3 Proportional contribution of each type of resource to the diet estimated by Bayesian lineal mixing models for each geographic area by a chronological period

Samples	Rhea and Lama		Rodents		C3 plants		Araucaria		Birds		Fish		Corn		Diet diversity
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Shannon H
SMza1	**0.294**	0.259	*0.201*	0.225	0.104	0.117	0.126	0.131	0.114	0.139	0.089	0.094	0.072	0.070	1.831
SMza2	*0.198*	0.210	0.131	0.152	**0.401**	0.148	0.105	0.101	0.092	0.106	0.039	0.048	0.034	0.039	1.651
NNqn1	**0.580**	0.174	*0.156*	0.152	0.045	0.055	0.155	0.105	0.025	0.032	0.022	0.025	0.017	0.019	1.280
NNqn2	**0.767**	0.196	0.040	0.067	*0.120*	0.111	0.038	0.054	0.018	0.027	0.010	0.014	0.007	0.010	0.864
CNqn1	0.065	0.077	*0.227*	0.309	0.035	0.046	**0.570**	0.234	0.034	0.050	0.035	0.045	0.033	0.038	1.297

The main resource for each area is displayed in bold, whereas the second resource is shown in italic

Particularly, the Bayesian mixing models suggest that the diet of human populations from South Mendoza was characterized by a high consumption of terrestrial animals (*Rhea-Lama* and rodents) in the earlier period, with a remarkable increase in the incorporation of C$_3$ plants after 1750 cal. BP. Overall, South Mendoza displayed the highest diversity of resources consumed in comparison with the samples from Neuquén. Our results are in agreement with the intensification process suggested for hunter-gatherers from South Mendoza during the Late Holocene (Neme 2007, 2009; Neme and Gil 2008). According to this, an imbalance between demographic density of human populations and the resources resulted in a greater pressure on resources of higher return, and thus, the diet was broadened to include a larger amount of low return resources, and new technologies for food processing were incorporated into the subsistence strategies. The occurrence of this process is supported by archeobotanical and some zooarcheological data (Giardina 2012; Llano 2011; Llano and Andreoni 2012; Llano and Ugan 2010; Neme 2007), although other studies have questioned some aspects of the faunal intensification (Fernández 2012; Otaola et al. 2015). Even though the consumption of birds, fishes, and corn has been proposed for South Mendoza (Giardina et al. 2014; Gil 2003; Novellino et al. 2004), the isotopes analyzed here suggest that their contribution to the diet of hunter-gatherers was very low. This contrasts with the relatively high percentage of aquatic resources expected from Binford's model and supports the previously informed overestimation of these resources for South America (Binford 2008). In agreement with our study, the archeobotanical evidence shows that the diversity and intensity of terrestrial plants exploited increased since 1900 cal. BP and also increased the frequency of species with low energy return such as *Condalia microphylla*, *Maihueniopsis darwinii*, and *Pterocactus tuberosus* (Llano 2015). The greater amount of seeds found in the archeological record of the Later Late Holocene is also taken as evidence of intensification due to the time and effort required for processing them (Llano 2015). This is accompanied by a trend towards the use of grinding stones and pottery around 1900 cal. BP (Neme 2007; Sugrañes 2011; Sugrañes and Franchetti 2012). In contrast, the previous period—4500–1900 cal. BP—is characterized by a low diversity of taxa, being predominant those that provide the greatest energy returns in the region such as *G. decorticans*, *Prosopis* sp., and *Schinus polygamus* (Llano 2011, 2015; Llano and Andreoni 2012). Interestingly, the increase in the proportion of C$_3$ plants is not associated with a higher frequency of caries throughout the Late Holocene (Novellino et al. 2004).

Demographic changes related to subsistence changes in South Mendoza have been assessed through the analysis of radiocarbon dates. This evidence shows a clear signal of a demographic increase around 1000 cal. BP, reaching a maximum size around 500 cal. BP (Gil et al. 2014). The

chronologies estimated for the increase in the demographic density and for the intensification process are not overlapping. Such disagreement could be attributed to sampling bias in the frequency of radiocarbon dates, as is suggested by the abrupt peaks observed in the distribution of frequencies for South Mendoza compared to northern areas (Gil et al. 2014). It should be kept in mind that these estimations of relative changes in population size based on radiocarbon dates cannot be compared with absolute demographic densities derived from the Binford's model. In consequence, further studies are needed to provide absolute estimations using evidence independent from the archeological record, such as DNA data (Ho and Shapiro 2011; Perez et al. 2016).

In Center Neuquén, the results of the Bayesian analyses suggest that during the period under study (6000–1750 cal. BP), the diets of hunter-gatherers were mainly composed of rodents and *Araucaria* with a lesser proportion of other resources. Thus, in agreement with the expectations of Binford's model, the diets were highly diverse and incorporated a significant proportion of plants. Zooarcheological evidence from Chenque Haichol cave, from which most of the human isotopes analyzed here were obtained, shows that species of small animals such as *Ctenomys* and *Galea* comprised the largest percentage of bone assemblages (80%), while *L. guanicoe* (guanaco) only accounted for a small proportion (Fernández 1988–1990). Other species of small terrestrial animals and freshwater resources from neighboring areas (*Diplodon patagonicus*) were also found in low proportion. Conversely, remains of *A. araucana* seeds were found in every level. The consumption of *Araucaria* seeds is supported by the presence of starch granules in 90% of the grinding stones found in Chenque Haichol cave, which suggests that the use of this resource can be traced back to 5500 cal. BP. Given the high productivity of *A. araucana* trees and the fact that the seeds are potentially available during large part of the year, this resource might have been an important component of the diets in Center Neuquén (Fernández 1988–1990). The high percentages of caries registered in the human remains recovered from this site are also in agreement with a diet enriched with carbohydrates (Kozameh and Barbosa 1988–1990). Based on this evidence and the values of δ^{13}C, it was suggested that despite their abundance in the zooarcheological record, rodents might have contributed in a small proportion to the diet (Fernández 1988–1990; Kozameh and Barbosa 1988–1990). This contrasts with the results obtained here using δ^{13}C and δ^{15}N.

The significant contribution of rodents and plants to the diet of hunter-gatherers from Center Neuquén, along with independent evidence that supports an increase in the population density, might suggest the occurrence of a process of intensification during the Middle-Late Holocene. In a recent work, we explored the relative and absolute demographic changes in northwest Patagonia through the analysis of mitochondrial

DNA (mtDNA) sequences and radiocarbon dates from Neuquén and Río Negro in Argentina and the regions of Bío Bío, Araucanía, and Los Lagos in Chile (Perez et al. 2016). Our results show a clear signal of a demographic increase around 5000 cal. BP for northwest Patagonia (Perez et al. 2016). The population density estimated for this region at the beginning of human peopling is, in average, similar to the baseline population density (TERMD2) values estimated by Binford's model (1–3 individuals/100 km^2). Then, the density increased, reaching the packing threshold proposed by Binford around 4000 cal. BP (10 individuals/100 km^2). To what extent these changes in population density gave rise to an intensification process, as it was suggested for other areas of North Patagonia (Favier Dubois et al. 2009; Stoessel and Martinez 2014), remains to be elucidated.

For North Neuquén, we found that the estimated contributions of different resources to the diet notably depart from the similar proportions of terrestrial animals and plants expected by Binford's model. Diets of this area are characterized by a significant consumption of *Rhea* and *Lama*, while the contribution of plants is negligible. The very low proportion of plants incorporated into the diet contrasts with the archeological record of this area for the first period under study (4800–1750 cal. BP). Grinding tools have been found in association with adult individuals in burial sites dated around 5000 cal. BP, suggesting an extended use of this technology (Aquihuecó and Hermanos Lazcano sites; Della Negra et al. 2009, 2014; Della Negra and Novellino 2005). Accordingly, analyses of the plant microremains preserved in these tools confirmed the processing of *Prosopis* (Lema et al. 2012). These evidences were interpreted as suggesting a more relevant role of C_3 plants than supported by the isotopic data analyzed here.

For the later sample from North Neuquén, which comprises individuals dated in the eighteenth century (i.e., Caepe Malal 1 and Andacollo sites), the intensive consumption of large herbivorous inferred from the isotopic values of human remains might be related to the incorporation of domestic animals, which have similar isotopic values to *Rhea* and *Lama* (Supplementary Table S1). Remains of horses and goats were found in Caepe Malal 1 and other historic archeological sites of North Neuquén (Béguelin et al. 2015; Hajduk and Biset 1996). Chronicles have documented the importance of horses not only in ritual contexts but also as a preferred food in Patagonia in historical times (Mitchell 2015). Additionally, the introduction of the horse changed the hunting techniques (with the use of balls of stones), which may have reduced the energetic cost for searching and catching of *Rhea* and *Lama*, increasing the consumption of these animals (Giardina 2010). The high proportion of animals incorporated into the diet, according to the isotopic values, contrasts with the high frequency of caries previously found in the same sample (Gordón and Novellino 2016). A possible explanation is that this frequency is not associated to a significant consumption of carbohydrates but to a reduction of dental wear compared to the previous period. Such reduction in dental wear could be attributed to changes in the techniques of food processing, as is suggested by the presence of pottery in this region since 1750 cal. BP (Gubevi site—Departamento Minas, and Michacheo site—Departamento Zapala; Della Negra 2008; Lema et al. 2012).

According to Binford's model (Binford 2001), only low-density populations (*unpacked*) can be sustained by the hunting of terrestrial animals. However, the presence of sites with high concentration of burials at the Middle-Late Holocene in North Neuquén suggests changes in the organization of hunter-gatherers that are coincident with the demographic increase around 5000 cal. BP, as inferred from radiocarbon dates and mtDNA, which reached a maximum of 20 individuals/ 100 km^2 by 1000 cal. BP (Della Negra et al. 2014; Perez et al. 2016). When population densities double the packing threshold, the subsistence projections controlled for density predict diets with a proportion of 0.25 of terrestrial animals and 0.75 of terrestrial plants (these values correspond to D2PHUNTP and D2PGATHP projections in EnvCalc). Overall, isotopic and demographic data suggest that, contrary to the expected by Binford's model for this environmental setting, the human groups from North Neuquén might have experienced a demographic increase with no intensification in the use of plants. Such departures from the model could be explained by local environmental conditions. Particularly, the carrying capacity of this area might be higher than the predicted by Binford's model on the basis of effective temperature solely. A higher capacity could, in turn, sustain larger populations of the main preys (*Rhea* and *Lama*) of human populations (Barberena 2013). Based on the current carrying capacity (La ganadería en Neuquén 2006) and the biomass of preys needed to support a carnivore (Carbone and Gittleman 2002), we estimated that the ecological setting of North Neuquén could support up to 18 humans/100 km^2 (this estimation assumes that the diet was exclusively based on terrestrial animals). Moreover, the seasonal movements of human groups following their preys (Hajduk and Lezcano 2007) might have also contributed to maximize the carrying capacity of the environment. For the later period, the evidence discussed here is in agreement with Binford's (2001) expectation that hunter-gatherers with horses depart from the projections derived from the model as a consequence of the changes in mobility and patterns of access to resources.

In sum, this study shows that the combined use of Binford's frames of reference and Bayesian mixing models is a solid approach for assessing the composition and proportion of resources consumed by human populations from northwest Patagonia in the Middle-Late Holocene. Across the whole region, prehistoric diets were highly variable throughout both time and space. Interestingly, a variety of subsistence

strategies seemed to be related to demographic changes that took place after 5000–4000 cal BP in the region under study: from the diversity in the use of resources in South Mendoza to the incorporation of a higher expected proportion of terrestrial animals in North Neuquén. The singularity of the samples from North Neuquén contrasts with the predicted intensification of plants as the basis of a population density increase for this kind of environmental settings. These findings open up new questions about the local conditions in North Neuquén that influenced regional variation in the diet and its relation with demographic changes during the Holocene. Two lines of inquiry that deserve further research in this context are the strategies of mobility that allowed the seasonal use of different ecological areas and the technology for food acquisition and processing that maximized the consumption of meat. Additionally, the demographic dynamic of the main prey (*L. guanicoe*) throughout the Holocene needs to be studied in detail to assess the availability of resources and its association with changes in the size of human populations.

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