Horticulturists and oxygen ecozones in the tropical and subtropical forests of Southeast South America

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We analyse the isotopic values (δ^{13}C, δ^{15}N) of the diet of pre-Columbian horticulturalist populations from tropical and subtropical areas of southeastern South America, belonging to the Guarani and Taquara archaeological units. The data indicate different trends in each one ($T = 4.21$; $P = 0.0004$), showing a mixed diet with maize consumption in the Guarani samples ($\delta^{13}C_{co} = -15.5 \pm 1.8$‰; $\delta^{13}C_{ap}$ -10.4 ± 0.8‰) and a depleted one in the Taquara ones ($\delta^{13}C_{co}$ -18.2 ± 1.7‰; $\delta^{13}C_{ap}$ -11.9 ± 0.9‰), with a significant internal dispersion in both populations. The first population has higher nitrogen values (δ^{15}N 11.1 ± 0.6‰) compared to the Taquara samples (δ^{15}N 9.3 ± 1‰), suggesting a more carnivorous diet. The recognition of these pre-Columbian mixed diets involves the identification of maize cultivation on the Atlantic side of the southernmost area of South America (Parana Delta, 34° SL). Through the analysis of δ^{18}O we have identified two isotopic ecozones, the first along the Paraná River Valley, with an average value of δ^{18}O -3.7 ± 0.5‰ (CV = 13.5%; CI = -3.83 / -3.16), and the second one, located in the Planalto of southern Brazil (Araucaria Forest), with a mean value of δ^{18}O -1.5 ± 0.3‰ (CV = 16.5%; CI = -1.69 / -1.29). The isotopic data (δ^{13}C, δ^{15}N and δ^{18}O) suggest human movements between these two ecozones.

Keywords: Carbon, Nitrogen, Oxygen, Isotopes, South America, Horticulturalists, Maize, Guarani, Taquara

Introduction

In this paper we present and compare for the first time the isotopic values (δ^{13}C, δ^{15}N) of the diets of two horticulturist groups from southeastern South America, which have been grouped into two late Holocene archaeological units: Taquara and Guarani. Both populations had variable horticultural components, including maize. The archaeological literature, however, is vague on this topic, and practically there is no formal data on the impact of maize or plants in the diet of these groups, or if there have been differences between them. While there are a few studies on the botanical remains recovered in archaeological contexts, these findings only allow us to ascertain that wild and cultivated plants were manipulated by these groups, but not their importance in their diet. In this regard, in this study we look to establish some formal parameters about the dependence of plants of both populations, the differences between them and the incidence of faunal resources. This study also contributes to the limited knowledge of the Formative Period of the region. Furthermore, it is the first isotopic approach to focus on the expansion of maize to the southern end of America on the Atlantic seaboard. This study also constitutes the first comparative analysis of humans recovered in Argentina and Brazil based on samples obtained from inland sites, overcoming the current political borders that have prevented the development of an archaeology based on a more regional approach. Additionally, we present an analysis of δ^{18}O values, characterising two isotopic ecozones in the study region, which allow us to evaluate the human mobility between them.

Archaeological and ethnographical background

The Taquara archaeological unit was constructed by Menghin (1957), who called it 'Eldoradense', having been initially identified in Eldorado, Misiones Province. It is the material expression of late

Holocene horticulturists groups distributed in the province of Misiones in Argentina and southern Brazil, which have been linked to the Kaingang and Xokleng ethnographic groups belonging to the Jê family linguistic group (Maybury-Lewis 1979; Urban 1992). Ten years after the pioneering work of Menghin, similar contexts were described as 'Itararé' (Chmyz 1967, 1968), as well as 'Taquara' in southern Brazil (Miller 1967, 1969; Schmitz and Becker 1991). The latter two terms have become popular in the archaeological literature. Here we use the term 'Taquara' for short. The archaeological unit comprises a variety of contexts and activities, such as quarries, agricultural work places, residential bases in caves, and open-air sites and pit-houses, especially in landscapes above 400 masl (Beber 2005; Carbonera 2014; Carbonera *et al.* 2015; Chmyz 1968, 1969; Corteletti 2012; De Masi 2005; Piazza 1969; Rizzo 1968; Rohr 1969, 1971; Schmitz 1988; Schmitz *et al.* 2010; Schmitz and Beber 2011; Schmitz and Rogge 2012). Pottery includes small-to-medium-size vases with high collars and thin walls, in dark to brown colours, made of a fabric consisting of sand and haematite. The pottery was decorated using dots and lines, as well as nail prints, vegetable basket marks, nets or corncob impressions (Araujo 2007; Beber 2005; Becker and Schmitz 1970; Carbonera 2014; Carbonera *et al.* 2015; Chmyz 1967; Menghin 1957; Miller 1969; Prous 1992). Mortuary practices include burial mounds surrounded by perimeter rings used for individuals with hierarchical positions, who were generally cremated prior to burial. Caves were also used to bury the dead, probably for commoners (Beber 2005; Copé 2006; Copé *et al.* 2002; De Souza and Copé 2011; Iriarte *et al.* 2013; Reis 2007; Rogge and Schmitz 2009; Schmitz *et al.* 2010; Schmitz and Beber 2011; Schmitz and Rogge 2012).

The Taquara complex is distributed between the 22° and 30° S parallels, and extends from the Atlantic coast to the Misiones province (Argentina) and the western portion of the State of Paraná in Brazil (Araujo 2007; Noelli 1999/2000; 2005). It might have existed in eastern Paraguay, but no archaeological research has been undertaken there. The ecological environments of this wide area include the ecotone of the Atlantic Coast – Coastal Forest (seashore – Serra do Mar Coastal Forest), the Araucaria Forest located in the Planalto ranging from 600 masl to 1800 masl and the Paraná Forest below 600 masl. On sites from the Atlantic coast, the economy was based on marine resources (Bastos *et al.* 2014, 2015; Colonese *et al.* 2014; Schmitz *et al.* 1993; Schmitz and Rogge 2012), while the inland area is much less documented. The almost invariable presence of charred seeds of *Araucaria angustifolia* found at the Planalto sites testifies its relative importance in the

local economy (Rogge and Beber 2013; Schmitz *et al.* 2010). Phytolith studies at the sites located there demonstrated the cultivation of *Zea mays* (maize), *Cucurbita* sp. (pumpkin), *Phaseolus* sp. (beans), *Manihot* sp. (cassava) and *Discorea* sp. (sweet potato) (Corteletti 2012; Corteletti *et al.* 2015). Unfortunately, we lack archaeofaunal data due to poor preservation conditions. At 3 de Mayo Cave, a Taquara site located in the Paraná Forest, the faunal collection includes *Tapirus terrestris* (tapir), *Tayassu* sp. (peccary) and *Mazama* sp. (mazama), as well as freshwater fish and small rodents (Loponte and Carbonera 2016b). The only vegetable resource identified is considered to be a palm (*Syagrus romanzzofiana*), which was intensely exploited by human groups in the Paraná Basin (Acosta and Ríos Román 2013; De Masi 2009).

In historical times, the Kaingang and Xokleng had diverse economies including the cultivation of maize, cassava and pumpkins, and the gathering wild plants, including *Araucaria angustifolia* seeds. Hunting targeted at least four species of monkey, peccaries, tapirs and several species of deer. Fishing and storage by smoking was also a common practice during the XIXth century. The villages usually had a population of between 50 and 100 individuals (Ambrosetti 1897; Borba 1908). The residential mobility of the Kaingang was adapted to yearly-based environmental productivity, restricted due to population density and influenced by the ownership of economic resources and symbolic landscapes (*i.e.* Iriarte *et al.* 2013). There is no information about the dimension of those territories. While each village possessed leaders, the authority of these was rather lax (Borba 1908).

The second horticulturalist group analysed here correspond to the Guarani archaeological unit, which was defined by Ambrosetti (1895) based on his field work in the province of Misiones. After this seminal work, all the archaeological properties related to this record were recognised by all the literature in Argentina (Capparelli 2015; Loponte and Acosta 2013; Lothrop 1932; Menghin 1962; Outes 1918; Sempé and Caggiano 1995; Torres 1911). Almost 70 years after the pioneering work of Ambrosetti, the Brazilian National Program of Archaeological Investigations again defined this archaeological unit in an almost identical way (Albuquerque 2008; Brochado 1984, 1989; Dias and Panachuk 2008; La Salvia and Brochado 1989; Milheira 2010; Noelli 2008; Pronapa 1970; Prous 1992; Rogge 1996; Scatamacchia 1990, 2008; Schmitz 1991; Schmitz *et al.* 1990). Today it is generally accepted that these contexts were produced by the ancestors of the historical Guarani, an Amazonian horticulturalist population linked to the exploitation of rainforest areas and

the ecotone between it, and the southeastern Atlantic coast of South America. Their place of origin would have been southwestern Amazonia, where the Tupi-Guarani linguistic family originates (Campbell 1997; Chousou-Polydouri *et al.* 2013; Chousou-Polydouri and Wauters 2013; Jensen 1999; Kaufman 1994; Rodrigues 1964, 2000). The maximum geographical range of this population was attained during the XVIth century between São Paulo State in Brazil and the Río de la Plata River in Argentina, a distance of nearly 2000km (Ambrosetti 1895; Brochado 1984, 1989; Chmyz 1983; Loponte and Acosta 2013; Noelli 1999/2000, 2008; Prous 1992; Schmitz *et al.* 1990; Sempé and Caggiano 1995).

The Guarani assemblages are identified by their very well-developed large vessels, with complex profiles and decorated alternately or in combination with three different ways: corrugated, nail-printed and painted in three different colours (red, white and black). The painted designs follow characteristic geometric patterns (Ambrosetti 1895; Prous 1992). Mortuary practices include large cemeteries, with burials in urns. The economy had an important agricultural component including maize, and numerous tropical species such as cassava (Brochado 1984; Noelli 1999/2000, 2008; Prous 1992). Faunal exploitation was quite diverse and linked to the specific environment of each site location, such as continental rainforest or coastal forest – seashore. The inland sites include the bones of terrestrial mammals such as *Mazama sp.*, *Ozotoceros bezoarticus* (pampas deer), *T. terrestris*, *Tayassu pecari – Pecari tajacu* (peccaries), *Blastocerus dichotomus* (marsh deer) and medium-to-small-sized rodents such as *Hydrochaeris hydrochaeris* (capybara) and *Myocastor coypus* (coypu), as well as freshwater fish. In coastal sites, marine resources were exploited (aquatic mammals, fish and molluscs) (Acosta and Mucciolo 2009; Capparelli 2015; Ferraso and Schmitz 2013; Loponte and Acosta 2003/2005; Loponte and Acosta 2013; Mucciolo 2007; Rogge 1996; Rosa 2006, 2010; Rosa *et al.* 2009; Schmitz *et al.* 1990; Schmitz and Ferraso 2011).

In historical times, the Guaraní had a complex economy including horticulture by slash and burn. The main crops were maize, cassava, beans, pumpkins and yams, complemented by other plants (peanut, tobacco, cotton, etc.). Fishing and hunting were also an important part of the economy. The species selected for hunting varied due to a specific environment (seashore, fluvial environments or inland forests). Guarani settlement pattern was sedentary. The residential camps including large huts used by extended families. Some villages comprised hundreds of individuals. These groups had a system of fission of the settlements, which is still not well understood, but allowed them to cover vast areas in a short time. This would

have allowed them to occupy a significant area of the forest of the southeastern South America relatively rapidly. The Guarani was a ranked society with chiefs, with effective power over the people, some of whom had political control in other villages along a vast territory, sometimes linked through kinship (Borba 1908; Ramírez, in Brochado 1984; Madero 1939; Schmidl 1948; Susnik 1961, 1975).

Several isotopic analyses have been carried out on individuals recovered from the Taquara sites located on the Atlantic seashore, where the diet was basically marine (Bastos *et al.* 2015; Colonese *et al.* 2014; De Masi 2001, 2009). There are also isotopic data from some individuals coming from sites located in the east of the Brazilian Planalto (De Masi 2009), which we will discuss in some detail in this paper. There are no available isotopic studies for the central and western Planalto, nor for the Paraná forest of Brazil and Argentina. For individuals recovered from the Guarani sites, there are some data obtained from the Paraná Delta, located in the lower basin, which show a mixed diet, with a significant intake of maize and depleted carbon proteins (Loponte and Acosta 2007, 2013, and see below).

The samples
In this paper we have included 32 individuals from different sites belonging to Taquara and Guarani located in these three distinct areas. Therefore, it is important to clarify the archaeological and ecological context of where they come from, and how they have been selected.

Taquara sites
The first Taquara site included is Abrigo do Matemático, a mortuary cave located near the city of São José dos Ausentes in the northeastern area of the State of Rio Grande do Sul (Brazil) at 1200 masl, in the Araucarian Forest (Miller 1971) (Fig. 1 and Table 1). At least 54 individuals were buried there (Brentano and Schmitz 2010; Izidro and Haubert 2003). Four of them were selected for this study, all adults over 18 years old. There are no radiocarbon dates available for this mortuary context, which was inferred based on its archaeological context to date from between 700 and 1800 years BP (Beber 2005).

The second site is the 3 de Mayo Cave, located near the left bank of the Paraná River, in the Paraná Forest ecological unit (province of Misiones, Argentina), at 100 masl (Fig. 1). It was excavated by Rizzo (1968), who recovered five burials (which have since been lost), and by the authors in 2013. The site has two levels of occupation. The most recent corresponds to the Taquara unit, dated to 777 ± 49 ^{14}C years BP (AA104530). The archaeological context indicates

Figure 1   Origins of the samples analysed in this work. 1: Arroyo Malo. 2: Arroyo Fredes. 3: Corpus. 4: Cueva 3 de Mayo. 5: Saltinho do Uruguai. 6: Abrigo do Matemático. 7: São Joaquim. 8: Urubici. 9: Alfredo Wagner. 10: Ribeirão da Herta.

multiple activities, including mortuary practices. We recovered some fragments of the feet of a buried individual located in the deepest section of the cave, which was previously excavated unsystematically by amateurs. They correspond to an adult whose sex could not be determined. The second sample to be analysed is a phalanx, recovered from the mouth of the cave. It is assignable to a human older than 14 years (cf. Scheuer and Black 2000), whose sex could not be determined.

The other individuals included in this study were recovered from the Taquara sites located in the Araucaria Forest above 600 masl, in the Brazilian Planalto: Urubici, São Joaquim, Alfredo Wagner and Ribeirão da Herta (Fig. 1). The isotopic data

for those individuals were obtained in the Geochemistry Center for Isotopes Studies (Lawrence Berkeley National Laboratory) and published by De Masi (2009). With the addition of these samples, we now have isotopic values for 14 individuals dating from 700 to 1800 ^{14}C years BP (Table 1).

Guarani sites
The Guarani samples were recovered from four different sites (Fig. 1 and Table 1). The first one, Saltinho do Uruguai, is located on the right bank of the upper Uruguay River in Águas de Chapecó County (Brazil), in the Paraná Forest, near the ecotone to the Araucaria Forest (Di Bitteti *et al.* 2003). It was accidentally discovered by a person using a bulldozer.

Table 1   Sites and dates of the samples analysed

Sites	Archaeological unit	Ecological unit	C14	*N*	Source
Saltinho do Uruguay	Guarani	Parana forest	470 ± 40[3] / 20 ± 60	6	Hoeltz y Brüggemann (2011)
Corpus	Guarani	Parana forest	495 ± 20	2	Loponte y Carbonera (2016a)
Arroyo Malo	Guarani	Parana Delta	S. XVI-XVII	2	Lothrop (1932)
Arroyo Fredes	Guarani	Parana Delta	690 ± 70[4] / 02 ± 40	8	Loponte et al. (2013)
Cave 3 de Mayo	Taquara	Parana forest	777 ± 49	2	Loponte y Carbonera (2016b)
Abrigo do Matematico	Taquara	Araucaria forest	700–1800 BP	4	Beber (2005)
Alfredo Wagner	Taquara	Araucaria forest	1610 BP (*)	1	De Masi (2009)
Riberao da Herta	Taquara	Araucaria forest	1290 BP (*)	1	De Masi (2009)
Sao Joaquim	Taquara	Araucaria forest	1180–1290 BP (*)	5	De Masi (2009)
Urubici	Taquara	Araucaria forest	1735 BP (*)	1	De Masi (2009)

(*) Dates with no sigma are reproduced following the original information, as published by De Masi (2009).

Rescue work carried out by a CRM company (Scientia Consultoria Científica) allowed the recovery of six burial structures containing eight individuals: three adults, three juveniles (between 12 and 20 years old; cf. Buikstra and Ubelaker 1994) and two infants, all buried in urns (Müller and Mendonça de Souza 2011). Two radiocarbon assays on human bones from this mortuary context yielded an age of 470 ± 40 ^{14}C years BP (Beta 226 116) and 320 ± 60 ^{14}C years BP (Beta 226115) (Caldarelli 2010; Hoeltz and Brüggemann 2011). The isotopic data presented here were taken from the fragments of the long bones of three adults and three juvenile individuals (>12 years old), with no gender information.

The second Guarani site, Corpus, is a large residential site located on the left bank of the Paraná River in the Misiones Province (Argentina), in the Paraná Forest (Fig. 1). It was excavated by the authors during two field seasons (Loponte and Carbonera 2016a). Two individuals were recovered from urns disrupted by fluvial action, both older than 18 years old, without sex determination. A radiocarbon date on one of them yielded an age of 495 ± 20 years ^{14}C BP (UCIAMS 134675). This date overlaps with another one of 459 ± 43 years ^{14}C BP (AA103647), obtained from a mammal bone recovered at the base of the archaeological level.

The third Guarani site is Arroyo Fredes, located on the Paraná Delta (Fig. 1). The archaeological deposit corresponds to a large residential site. The initial excavations were carried out by technicians from the Museum of Natural Sciences of La Plata in the early twentieth century, who recovered several burials. Four of them (AFR6869, AFR6858, AFR6856 and AFR6857), all adults without their sex being established, were analysed for this study. The remains of one individual (6865/L11) was dated to 690 ± 70 years ^{14}C BP (UGA 10789) (Loponte and Acosta 2007). Two more individuals were recovered from our excavations in 2002/2003 (Loponte and Acosta 2003/2005) (acronyms AFE-1 and AFE-2). One of them was an adult male, which was dated to 370 ± 50 years AP [14]C (LP-1428). The second individual was possibly an adult female.

The fourth Guarani site is Arroyo Malo, located close to Arroyo Fredes in the Paraná Delta. It was also excavated by technicians from the Museum of Natural Sciences of La Plata in the early twentieth century and later by Lothrop (1932), who published limited information about the site. The archaeological context seems to be represented by mortuary practices rather than by domestic activities. Some glass beads associated with the archaeological context suggests an initial stage of contact with Europeans, thus it can be assigned to the sixteenth century or the first half of the seventeenth century. The samples analysed here correspond to two adults buried in different urns (Loponte and Acosta 2007). Taken together, the samples recovered from the Guarani sites included in this study correspond to 18 individuals ranging from 690 ± 70 to 320 ± 60 ^{14}C years BP (Table 1).

Ecological aspects and regional isoscape
Landscape
The sites included in this study are located in three different landscape units. The southernmost is the Paraná Delta (see location in Fig. 1), which is a subtropical wetland, with an average precipitation of 1000 mm per year and without a dry season. A multi-layered riparian forest with a continuous canopy with a height of 8–15 m, associated with riverine prairies highly fragmented by streams has developed there (Cabrera 1976; Kalesnik *et al*. 2008; Roesler and Agostini 2012). Most of the vegetation and the sources of the fluvial energy have a C_3 pattern (Madanes *et al*. 2013; Marchese *et al*. 2014).

The second landscape unit is the Paraná Forest, consisting of a multilayered rainforest that develops up to 600 masl with a moss layer to the ground, a shrub of three successive layers, with a continuous canopy between 10 and 20 m up to 30–40 m, which limits the amount of light reaching the soil surface (Cabrera 1976; Di Bitetti *et al*. 2003; Martínez Crovetto 1963; Moscovich *et al*. 2010). Rainfall varies between 1700 and 2400 mm annually, without a dry season (Rodríguez *et al*. 2005). While it is a tropical and subtropical area, most of the coverage of grasses, shrubs and trees are within a C_3 photosynthetic pathway (Powell and Still 2009; Powell *et al*. 2012) (Fig. 1).

The third landscape unit is the Araucaria Forest, located in the Brazilian Planalto, which develops from 600 masl to 1800 masl. This region is characterised by open grass fields with large areas of *Araucaria angustifolia* forest 18–20 m tall, which includes low trees of several species, shrubs and offspring of *A. angustifolia*. Here the climate is temperate, with 1800 mm of rainfall annually (Silva *et al*. 2009). The isoscape is within a C_3 photosynthetic pathway (Powell and Still 2009; Powell *et al*. 2012) (Fig. 1).

Palaeoenvironmental conditions
The current climate of both the Paraná and Araucarian Forests would have been established by around 4000 years BP (Buso Junior *et al*. 2013; Pessenda *et al*. 2009). The forest, which colonised the open fields of Planalto, began to expand after a while (<3000 years BP), perhaps helped by human activity, i.e. burning of fields and the generation of productive patches in the landscape (Behling 1993, 1995, 1997, 1998, 2002; Behling and Pillar 2007; Bitencourt and Krauspenhar 2006; Eskuche 2007;

Ledru *et al.* 1998; Zech *et al.* 2009). In the Paraná Delta, the archaeological data show a similar climate to the current one which were established by at least 2300 years BP (Loponte *et al.* 2012).

Stable isotopes

The application of stable isotope analysis for understanding the human diet began in the last quarter of the last century (De Niro 1985; De Niro and Epstein 1978a, 1978b, 1981; Krueger and Sullivan 1984; Schoeninger and De Niro 1984; Sullivan and Krueger 1981; Tieszen *et al.* 1983; van der Merwe and Vogel 1978, among others). Since then, the growth of this research area has been exponential and it is impossible to mention all the publications, even just those presenting major methodological developments. One of the key aspects to understanding this success is that the isotopic values obtained from collagen and apatite are an average of an individual's diet for the last 7–10 years of their life (Ambrose 1993), thus offering a realistic vision of long-term food habits, rather than episodic intakes of food. However, the main limitation of this method is that it cannot identify the specific resources consumed, only broad categories.

Numerous studies have shown that the values of $\delta^{13}C$ measured in collagen ($\delta^{13}C_{co}$ from now on) are enriched by about 5‰ compared with the values of their diet. Thus, plant-based diets with C_3 photosynthetic patterns yield values of -21‰, while those with monoisotopic C_4 photosynthetic pathways present values of ~ 7‰ (De Niro and Epstein 1978a, 1978b; Koch 2007; Krueger and Sullivan 1984; Lee-Thorp *et al.* 1989; Vogel 1978a, 1978b; Vogel and van der Merwe 1977). In the inorganic fraction ($\delta^{13}C_{ap}$ from now on), monoisotopic diets show magnitudes of ~ 13.5‰ and ~ 3‰, respectively (Kellner and Schoeninger 2007; Lee-Thorp and van der Merwe 1987; Sullivan and Krueger 1981).

Different studies have also shown that collagen carbon values mainly reflect the content of the protein intake, while those from apatite have a closer relation to the total diet (protein + fat + carbs) (Ambrose and Norr 1993; Katzenberg 2008; Krueger and Sullivan 1984). This means that differences between the two carbon sources ($^{13}\Delta$ from now on) largely reflect the intake of plants. This model, developed by Krueger and Sullivan (1984), is used as an indicator of the trophic level of diets and / or to identify the marine components therein (Ambrose and Krigbaum 2003; Ambrose and Norr 1993; Ambrose *et al.* 1997, 2003; Harrison and Katzenberg 2003; Lee-Thorp *et al.* 1989; Loftus and Sealy 2012; Norr 1995; Pate 1995; Rand *et al.* 2013; Roksandic *et al.* 1988; Waterman *et al.* 2015; White *et al.* 2001). After several empirical tests, the results show that

wider spacing is typical of herbivores, with mean values of 6.8 ± 1.4‰, while a carnivorous diet is ≤ 4‰ ± 1‰ (Ambrose and Krigbaum 2003; Ambrose and Norr 1993; Clementz *et al.* 2009; Krueger and Sullivan 1984; Lee-Thorp *et al.* 1989; Loftus and Sealy 2012). However, there are no absolute values for demarcating thresholds but it should be defined empirically according to the particular context analysed (Ambrose and Norr 1993; Kellner and Schoeninger 2007). The thresholds also depend on the combination of photosynthetic proteins and carbohydrates ingested (Ambrose and Krigbaum 2003; Ambrose and Norr 1993; Ambrose *et al.* 2003; Cormie and Schwarcz 1996; Kellner and Schoeninger 2007; Metges *et al.* 1990; Schwarcz *et al.* 1999; Stevens *et al.* 2008; van Klinken *et al.* 1994). Normally this spacing scheme, except for some particular contexts, is consistent and it has been proven empirically in many studies, and it is reinforced when used in conjunction with the nitrogen values. Indeed, $\delta^{15}N$ increases as the body intakes foods of higher trophic levels at a rate of 3–4‰ (Bocherens and Drucker 2003; Hedges and Reynard 2007; Schoeninger and De Niro 1984). Thus, the combination of both isotopes of carbon and nitrogen is used to estimate the trophic position of individuals (Ambrose and Norr 1993; Ambrose *et al.* 1997, 2003; Froehle *et al.* 2010, 2012; Hedman *et al.* 2002; Loftus and Sealy 2012; Warinner and Tuross 2009).

Based on laboratory experiments, Kellner and Schoeninger (2007) suggested that isotopic analysis is more reliable if lines of regression are used on both values of $\delta^{13}C_{co}$ and $\delta^{13}C_{ap}$. Some authors have suggested that this model has methodological limitations related to metabolic aspects and the intake of other nutrients that are not included in the analysis of controlled diets, as well as a lack of consideration for the values of nitrogen (Froehle *et al.* 2012; Loftus and Sealy 2012; Warinner and Tuross 2009). To avoid some of these problems, Froehle *et al.* (2012) developed a multivariate model incorporating the values of $\delta^{15}N$ from the calculation of discriminant functions, which are plotted in clusters of known diets. This allows a more accurate evaluation of isotopic diets, especially those that incorporate C_4 plant foods such as maize, which constitutes a very large field of investigation within isotopic analysis (Ambrose *et al.* 2003; Balasse *et al.* 1999; Boyd *et al.* 2008; Calo and Cortés 2009; Froehle *et al.* 2012; Gheggi and Williams 2013; Gil *et al.* 2010; Hart *et al.* 2011; Killian *et al.* 2012; Laguens *et al.* 2009; Metcalfe *et al.* 2009; Rand *et al.* 2013; Scherer *et al.* 2007; Slovak and Paytan 2009; Staller *et al.* 2006; Stronge 2012; Tykot 2002, 2004; White *et al.* 2006).

Oxygen values are used in identifying the spatial locations where individuals developed their lifecycle. Oxygen is incorporated into bone tissue by water intake, directly and through food, which precipitates links to $(PO_4)^{-3}$, $(CO_3)^{-2}$ and OH^- in the bioapatite. The link between P and O is chemically more stable and robust against diagenetic alteration and isotopic exchange in low-temperature depositional environments (Balasse *et al.* 2002; Grimes and Pellegrini 2013; Regnier *et al.* 1994), and it contains between 85% and 95% of the oxygen atoms (Brady *et al.* 2008). Oxygen is incorporated by metabolic processes, largely retaining the isotopic source signal influenced by temperature, the amount of water that precipitates annually and the lifestyles of organisms, among which are the frequency of water intake and the components of the diet, etc. (Bocherens *et al.* 1996; Bryan *et al.* 1996; Dansgaard 1964; De Niro and Epstein 1981; Grimes and Pellegrini 2013; Hobson 1999; Kohn *et al.* 1998; Longinelli 1984; Sponheimer and Lee-Thorp 1999).

The analysis of human mobility based on $\delta^{18}O$ in the enamel and bone bioapatite has been applied in numerous studies (Britton *et al.* 2015; Dobney *et al.* 2007; Eerkens *et al.* 2014; Evans *et al.* 2006; Knudson and Price 2007; Sánchez Canadillas 2014; Stuart-Williams *et al.* 1996; White *et al.* 2000). We still have no archaeological applications in the region we are studying, and there have been no isotopic zones identified as in other parts of the world (e.g. Montgomery *et al.* 2009). However, studies on the oxygen content of local waters are available (Albero and Panarello 1980; Cruz *et al.* 2005, 2006; Dapeña and Panarello 2005; Gastamns *et al.* 2010; Panarello and Dapeña 2009), which allow us to explore the isotopic values of humans and prey in archaeological contexts.

The isotopic analysis we carried out for this study was performed at the Environmental Isotope Laboratory of the University of Arizona (EIL) and the SIRFER Laboratory at the University of Utah. A small number of analyses were carried out at the Center for Applied Isotope Studies (CAIS-UGA) at the University of Georgia (USA), at the Institute of Geochronology Isotope (INGEIS-CONICET – AIE) in Argentina, and the Department of Earth System Science at the University of California (UCIAMS). All the samples selected for this study were fragments of compact bone tissue. The samples have the acceptable parameters of wt %C and wt %N (>13% and >4.8%, respectively). For the analyses based on collagen, only samples with adequate quantities of this element were retained for analysis (>1%; cf. van Klinken 1999) and within a ratio C/N between 2.9 and 3.6 (Ambrose 1990; De Niro 1985). The removal of diagenetic carbonates followed the pre-treatment

methods described in Koch *et al.* (1997), removing the adsorbed carbonate, which is more soluble than the structural carbonate and increases the reliability of the readings for the paleodietary analysis (Ambrose and Krigbaum 2003; Garvie-Lok *et al.* 2004; Grimes and Pellegrini 2013; Krueger 1991; Lee-Thorp and van der Merwe 1987, 1991; Tykot 2004).

The values for $\delta^{15}N$ and $\delta^{13}C_{co}$, as well as the carbon and nitrogen content, were measured on a continuous-flow gas-ratio mass spectrometer. The samples were burned using an elemental analyser coupled to a mass spectrometer. The standardisation is based on acetanilide for elemental concentration, NBS-22 and USGS-24 for $\delta^{13}C$, and IAEA-N-1 and IAEA-N-2 for $\delta15N$. The precision is better than ± 0.08 for $\delta^{13}C_{co}$ and ± 0.2 for $\delta15N$ ($\pm1\sigma$), based on repeated internal standards.

The values for $\delta^{18}O$ and $\delta^{13}C_{ap}$ were measured using an automated carbonate preparation device coupled to a gas-ratio mass spectrometer. The powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C in the presence of silver foil. The isotope ratio measurement is calibrated based on repeated measurements of NBS-19 and NBS-18, and the precision is $\pm 0.1‰$ for $\delta^{18}O$ and $\pm 0.08‰$ for $\delta^{13}C_{ap}$ ($\pm1\sigma$).

Some samples showed a significant diagenesis, so the collagen values were discarded and only the inorganic fraction values were used (Table 3). This could also have been impacted to some degree by an eventual transfer of the carbon of atmospheric CO_2, which is enriched, as well as by the process of the transfer of CO_2 from the ground, which is a depleted substrate (cf. Powell *et al.* 2012). In this study we used the isotopic values of fish and seeds obtained from modern samples. We applied a time-dependent correction due to the Suess-effect of $-0.005‰$ per year between 1860 and 1960, and $-0.022‰$ per year since 1960 (Chamberlain *et al.* 2005) until 2013, when the modern samples were collected (Francey *et al.* 1999; Indermühle *et al.* 1999). This correction provides an approximate value of $\delta^{13}C$ for comparing ancient and modern ecosystems. Finally, we must consider some degree of impoverishment in the values of $\delta^{13}C$ due to the canopy effect that occurs in the Paraná Forest in particular (cf. Farquhar *et al.* 1982; Franco *et al.* 2005; van der Merwe and Medina 1991).

Prey

All the mammals identified in the inland Taquara and Guarani sites have diets based on C_3 resources, except *H. hydrochaeris*, which has a mixed diet. Their nitrogen values show typical levels of continental diets (Table 2). Freshwater fish are quite important in the region under study, especially *Prochilodus lineatus*, which represents more than 50% of the fish biomass

Table 2 Isotopic values for the bones of the main prey

Taxon	Common name	N	Area	$\delta^{13}C_{co} \pm 1\,\sigma$	$\delta^{13}C_{ap} \pm 1\,\sigma$	$\delta^{15}N \pm 1\,\sigma$	Source
Ozotoceros bezoarticus	Pampas deer	3	1–2–3	−21.1 ± 1.1	−10.9 ± 1.5	5.2 ± 0.4	(1)
Myocastor coypus	Coipo	7	1–2–3	−20.1 ± 1.6	−9.1 ± 3.1	5.4 ± 1.5	(1)
Blastocerus dichotomus	Marsh deer	24	1–2–3	−21.1 ± 1.4	−10.3 ± 1.4	5.6 ± 0.6	(2)
Mazama sp.	Brocket	2	1–2–3	−23.8 ± 1.1		9.0 ± 0.8	(4)
Hydrochaeris hydrochaeris	Capibara	19	1–2–3	−16.2 ± 2.7		4.8 ± 0.6	(5)
Tapirus terrestris	Lowland tapir	1	1–2–3	−21.8		2.4	(6)
Tayassu sp.	Peccary	7	1–2	−21.7 ± 1.0		8.3 ± 3.8	(1) (4) (6)
Cuniculis paca	Lowland paca– agutí	1	1	−20.8		7.9	(4)
Alouatta sp.	Monkeys	4	1	−22.0 ± 0.5		–	(4)
Prochilodus lineatus	Shad	112	1–2–3	−24.5 ± 3.0		8.3 ± 1.2	(1)
Leporinus obtusidens	Boga	1	1–2–3	−22.4		6.1	(1)
Pterodoras granulosus	Granulated catfish	2	1–2–3	−20.8 ± 4.5		7.5 ± 2.8	(1) (3)
Pimelodus maculatus	Yellow catfish	3	1–2–3	−23.3 ± 1.8		8.5 ± 1.0	(1)
Hoplias malabaricus	Wolf fish	2	1–2–3	−24.2 ± 0.9		8.9 ± 0.3	(1)
Salminus brasiliensis	Dorado	3	1–2–3	−24.0 ± 0.9		7.9 ± 0.1	(1)
Ageneiosus brevifilis	Slopehead catfish	3	1–2–3	−23.6 ± 0.1		8.3 ± 0.7	(1)
Pseudoplat. reticulatum	Shovelnose	3	1–2–3	−25.6 ± 0.2		8.7 ± 0.5	(1)
Araucaria angustifolia	Araucaria tree	29	2–3	−27.8 ± 1.0		4,1 ± 1.2	(7)
Syagrus romanzoffiana	Pindo Palm	3	1–2–3	−25.1 ± 0.8		3.8 ± 0.3	(1) (6)

Note: The values in the 'N' column (sample size) correspond to the $\delta^{13}C_{co}$ determinations. For the other sample sizes, see the cited texts. The 'Area' column refers to the environmental availability of each resource. 1 = Paraná Forest. 2 = Paraná Delta. 3 = Araucaria Forest.

Sources: (1) This paper; (2) Loponte and Corriale (2012); (3) Loponte (2008); (4) Colonese *et al.* (2014); (5) Corriale and Loponte (2015); (6) De Masi (2009); (7) Franco *et al.* (2005). The modern fish and seed values are corrected by the Suess-effect.

of the Paraná River. Unfortunately, no bone collagen values are available for this or for other significant species in archaeological terms. In Upper Paraná *P. lineatus* showed values for muscle tissue ranging between $\delta^{13}C_{co}$ −24.8 ± 3‰ and −31.5 ± 2.6‰ (Lopes *et al.* 2007), with an average of −27.5‰. Another analysis conducted by Marchese *et al.* (2014) in the middle Paraná gave a similar average (−27.3 ± 3.1‰). Because the values were obtained from muscle tissue, which is depleted by 1.1–1.6‰ compared to bone collagen in fish (Sholto-Douglas *et al.* 1991), we can consider an approximate mean value of $\delta^{13}C$ −26.0 ± 3‰ in collagen to be −24.5 ± 3‰ when corrected for the Suess-effect. The values of $\delta^{15}N$ obtained in muscle tissue were also corrected in this study by −2.35‰ (cf. Sholto-Douglas *et al.* 1991) (Table 2).

Other fish species identified in the archaeological record, such as *Pterodoras granulosus, Leporinus obtusidens, Pimelodus maculatus, Hoplias malabaricus, Salminus brasiliensis, Ageneiosus brevifilis* and *Pseudoplatystoma reticulatum* (Acosta and Mucciolo 2009; Loponte 2008; Musali 2010), also showed depletion, with an average value of $\delta^{13}C$ −26.7 ± 1‰ and $\delta^{15}N$ 10.0 ± 1‰ in muscle tissue (calculated on the basis of Saigo *et al.* 2015: Table 2). Thus, for these species we consider a bulk value for bone collagen to be −25.4 ± 1‰ (Suess-corrected −23.6‰) and 8 ± 1‰ for nitrogen.

One of the most exploited wild plant species in the three landscape units analysed (*Araucaria angustifolia* and *Syagrus romanzoffiana*) also have a C₃ pattern, like the majority of the wild plant resources (Madanes *et al.* 2013).

Results

The analysis yielded about 54 new isotopic values plus 25 already published related to the diet from humans from both archaeological units, excluding 12 results corresponding to the organic fraction of individuals from Saltinho do Uruguai, which were discarded because the C/N ratio was outside the range of reliability (Ambrose 1990; De Niro 1985) (Table 3).

Carbon and nitrogen

The results obtained for collagen show different trends for each archaeological unit (*t*-Student; T = 4.21; P = 0.0004). The Guarani individuals show an enriched diet (*n* 11, $\delta^{13}C_{co}$ = −15.5 ± 1.8‰), excluding the SCE02 sample, which clearly stands as an outlier (see Table 2 and Fig. 2). The second one is represented by the Taquara samples (*n* 13, $\delta^{13}C_{co}$ −18.2 ± 1.7‰), excluding here again another outlier (RA-05; Table 2 and Fig. 2). In apatite, both groups also reflect different trends (Wilkinson test: W = 8; P = 0.012), enriched in Guarani [$\delta^{13}C_{ap}$ (*n* 14) −10.4 ± 0.8‰] and more depleted in Taquara [$\delta^{13}C_{ap}$ (*n* 4) −11.9 ± 0.9‰].

Beyond the general trends observed above, there is some variability in the Taquara samples. For example, individuals recovered from 3 de Mayo Cave and two from the Sao Joaquin (RA-01 and RA-05) site show enriched values (*n* 4, $\delta^{13}C_{co}$ −14.6 ± 2.6‰). None of these individuals have levels of $\delta^{15}N$ that suggest marine diets, so the magnitudes should be enriched by maize intake (see also De Masi 2001, 2009), which is recorded in the environment of adjacent areas at least from 1900 ¹⁴C years BP (Behling *et al.* 2005; Gessert *et al.* 2011). Moreover, an enriched charred residue stuck into one ceramic vessel was

Table 3 Isotopic values of humans

|	Sites	ID sample	ID Lab.	Age	$\delta^{13}C_{co}$ (‰)	$\delta^{13}C_{ap}$ (‰)	$\Delta^{13}C$	$\delta^{15}N$ (‰)	C/N	Source
Guarani	Parana delta	Arroyo Fredes	AFR6869	Sirfer 13-2299	Adult	−14.3	−10.2	4.1	10.5	3.1	(1)
		Arroyo Fredes	AFR6858	Sirfer 13-2300	Adult	−14.7	−10.1	4.6	10.8	3.4	(1)
		Arroyo Fredes	AFR6856	Sirfer 13-2301	Adult	−17.1	−12.5	4.6	12.2	3.2	(1)
		Arroyo Fredes	AFR6857	Sirfer 13-2302	Adult	−12.9	−9.9	3.0	11.4	3.2	(1)
		Arroyo Fredes	AFE-2	EIL-1003	Adult	−16.4	−9.9	6.5	10.9	3.5	(1)
		Arroyo Fredes	AFE-1	EIL-1004	Adult	−16.8	−9.3	7.5	10.3	2.9	(1)
		Arroyo Fredes	AF 6865/L11	UGA 10789	Adult	−16.7			11.2	2.9	(2)
		Arroyo Fredes	AF 7681-L/8-19	AIE 12364	Adult	−15.1				3.0	(2)
		Arroyo Malo	AM 6630/T4-16	AIE 11719/25	Adult	−15.2	−10.2	5.0		3.1	(2)
		Arroyo Malo	AM 6631/T5-11	AIE 12365/409	Adult	−15.2	−10.1	5.1		3.2	(2)
	Parana forest	Corpus	SCE01	UCIAMS 134675/1	≥18 years	−16.5			11.6	3.3	(1)
		Corpus	SCE02	UCIAMS 134675/2	≥18 years	−10.9			16.4	3.1	(1)
		Saltinho do Uruguay	1 ACHSU3C2	EIL-2000	Adult	−19.5	−10.3		10.2	5.9	(1)
		Saltinho do Uruguay	2 ACHSU3C2	EIL-2001	Adult	−20.3	−10.8		8.4	5.7	(1)
		Saltinho do Uruguay	3 ACHSU3C2	EIL-2002	Adult	−23.1	−10.4		11.2	14.1	(1)
		Saltinho do Uruguay	4 ACHSU3C2	EIL-2003	Juvenile	−19.6	−11.3		10.1	6.0	(1)
		Saltinho do Uruguay	5 ACHSU3C2	EIL-2004	Juvenile	−21.8	−10.2		8.4	8.5	(1)
		Saltinho do Uruguay	6 ACHSU3C2	EIL-2005	Juvenile	−23.9	−9.8		9.4	15.2	(1)
Taquara	==Araucaria forest==	Cueva 3 de Mayo	G3M-I1	EIL-2011	Adult	−16.5			12.6	3.2	(1)
		Cueva 3 de Mayo	G3M-I2	EIL-2012	>14 years	−16.1			11.3	2.9	(1)
		Abrigo do Matemático	AM-1	EIL-2007	Adult	−18.9	−11.8	7.1	9.0	2.8	(1)
		Abrigo do Matemático	AM-2	EIL-2008	Adult	−20.7	−12.8	7.2	9.1	3.2	(1)
		Abrigo do Matemático	AM-3	EIL-2009	Adult	−19.9	−12.3	7.7	10.4	3.2	(1)
		Abrigo do Matemático	AM-4	EIL-2010	Adult	−20.0	−10.7	9.3	9.2	2.9	(1)
		Alfredo Wagner	AW-01	CAMS 53916	nd	−17.9			7.6	(*)	(3)
		Riberao da Herta	SC-VI-1 6	CAMS 53 11 4	nd	−18.6			9.5	(*)	(3)
		Sao Joaquim	RA-01	CAMS 51673	nd	−15.1			10.4	(*)	(3)
		Sao Joaquim	RA-03	CAMS 5414 2	nd	−18.1			8.1	(*)	(3)
		Sao Joaquim	SJ -04	nd	nd	−20.6			8.7	(*)	(3)
		Sao Joaquim	RA-05	CAMS 51674	nd	−10.8			7.7	(*)	(3)
		Sao Joaquim	RA-06	CAMS 54143	nd	−17.2			8.2	(*)	(3)
		Urubici	UR-01	CAMS 53915	nd	−17.1			8.9	(*)	(3)

Sources: (1) This paper; (2) Loponte and Acosta (2007); (3) De Masi (2009). (*) Amounts reported at the generic level within the range 2.9–3.6 (after De Masi 2009). The values in grey are outside the ratio C/N 2.9–3.6.

dated to 2285 cal. years BP at a site in the Planalto (De Masi 2006). In contrast, samples from the Araucaria Forest are depleted (n 10, $\delta^{13}C_{co}$ −18.0 ± 2.9‰). It should be noted that there may be a chronological component in these differences, but more dates are needed to explore this possibility.

The spacing values of the carbon sources also show two distinct trends ($W = 40$; $P = 0.016$). The Guarani samples have a lower average (n 8, $\Delta^{13}C$ 5.0 ± 1.4‰) than those obtained from the Abrigo do Matemático, the only Taquara site with available data (n 4, $\Delta^{13}C$ 7.8 ± 1‰). Similarly, there are significant differences in nitrogen ($T = 4.05$; $P = 0.0006$). The first population has higher values (n 8, $\delta^{15}N$ 11.1 ± 0.6‰, excluding SCE02, see below) when compared with the second one (n 14, 9.3 ± 1‰), suggesting a more carnivorous diet for the Guarani individuals (Fig. 3). The values of $\delta^{13}C_{co}$ and $\delta^{15}N$ show strong positive linear correlations ($r = 0.75$; $P = 0.001$), in the same way that the $\Delta^{13}C$ and $\delta^{15}N$ values do ($r = 0.77$; $P = 0.001$), indicating a progressive increase in protein intake, from pure herbivores to the most carnivorous diets of the Amazonian horticulturalists (Figs. 3 and 4).

The nitrogen levels observed in the Taquara and Guarani samples reflect continental diets (cf. Schoeninger and De Niro 1984). However, individual SCE02 from Corpus behaves like an outlier in $\delta^{13}C_{co}$ (−10.9‰) and $\delta^{15}N$ (16.4‰). Both values are typical of a marine diet, close to those obtained from
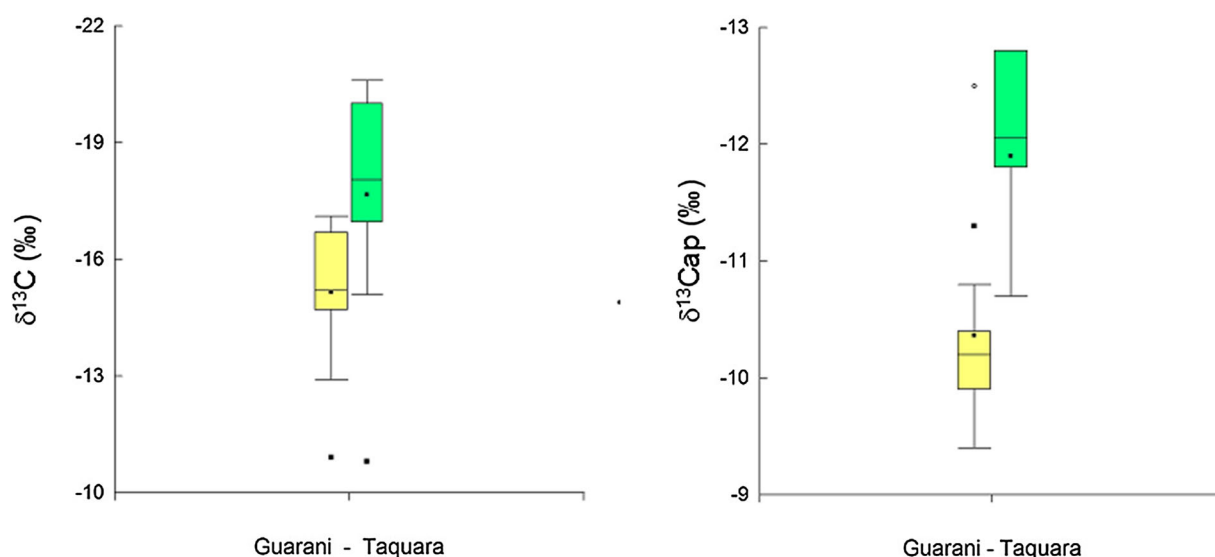
Figure 2   Dispersion values of $\delta^{13}C_{co}$ (‰) and $\delta^{13}C_{ap}$ (‰) of the samples from the Guarani and Taquara sites.

individuals recovered from the Atlantic seashore of Santa Catarina (Bastos *et al.* 2014, 2015; Colonese *et al.* 2014; De Masi 2009). Therefore, this could be the first isotopic evidence of population movements between the upper Paraná basin and the Atlantic coast, 650 km to the east (Fig. 4).

Regardless of this specific individual and the two samples RA-01 and RA-05, when considering the collection analysed as a whole, it is quite clear that there were two distinct continental diets. The first developed in the Araucaria Forest, pertaining to the archaeological Taquara unit, based on depleted proteins and carbohydrates. The second one developed in the Paraná Forest, linked to the Taquara and Guarani archaeological units and to the latter in the Paraná Delta, which was based on equally depleted carbon proteins, but with an important consumption of C_4 carbohydrates. Since we lack accurate dates for most of the samples from the Araucaria Forest, we do not know if there is any chronological bias (see Figs. 4 and 5).

To get a clearer picture of the differences between the human values from both archaeological units, we used the linear dietary model proposed by Kellner and Schoeninger (2007) and the discriminant functions developed by Froehle *et al.* (2012). Individuals recovered from Abrigo do Matematico (Taquara unit) show 70–100% of their intake was related to C_3 proteins and energy. By contrast, the Guarani samples fall between the two protein lines, showing values that are more diagnostic of a mixed diet (Figs. 5 and 6).

The values of a few samples could be used to calculate the discriminant functions (see Table 3).
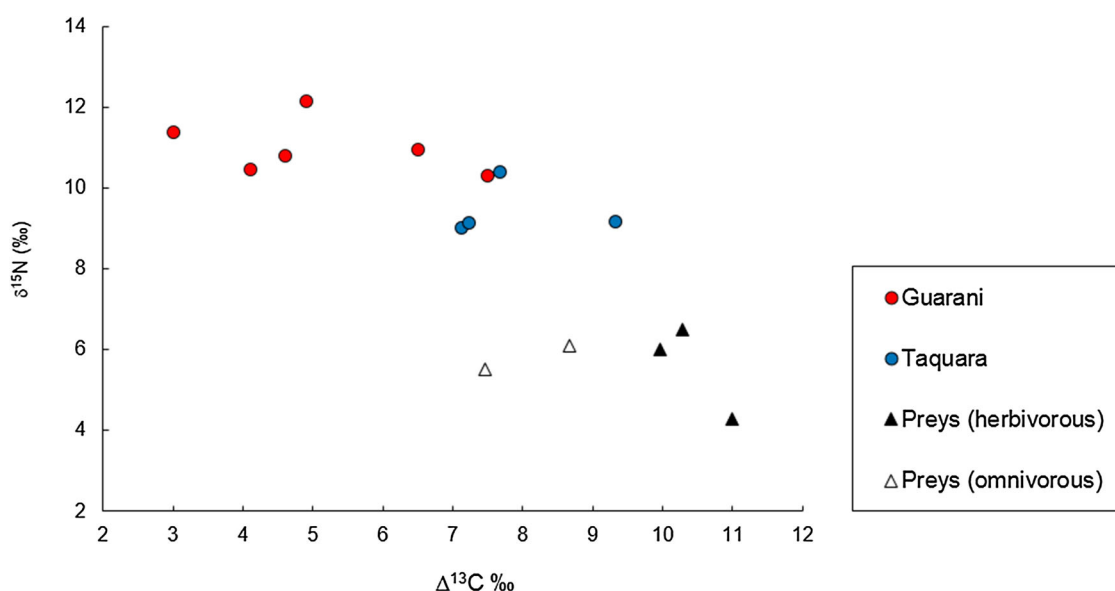
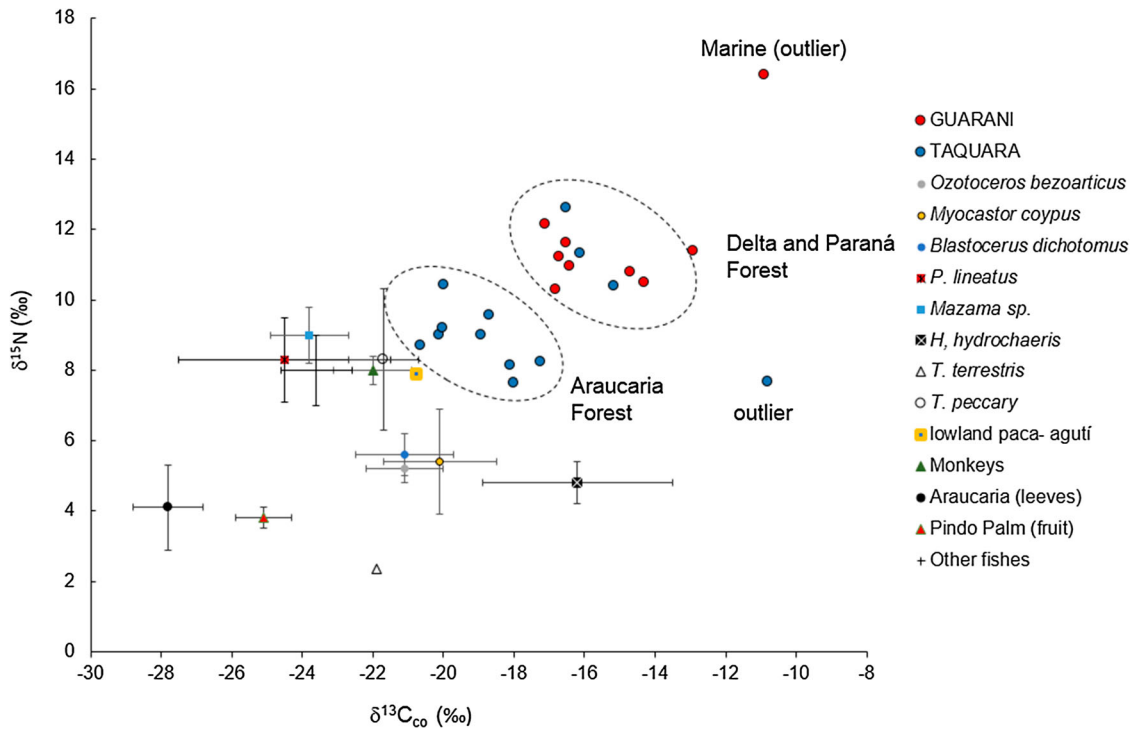**Figure 3**   Values of $\Delta^{13}C$ and $\delta^{15}N$ values.

Figure 4 Dispersion values of $\delta^{13}C_{co}$ and $\delta^{15}N$.

Hopefully, this database will increase substantially in the near future. For now, the averages (±1σ) of function 1 mark a clear gap between these two archaeological units (based on inland samples) (Fig. 7), which may reflect in part the current state of sampling, but also genuinely different trends.

To conclude this section, two other aspects must be pointed out. First, since the two populations considered formed hierarchical societies, it is expected that differences will be found in the food intake according to the social status of the analysed individuals. The isotopic data available from the Taquara contexts come from mortuary caves, which suggests that these individuals did not have a high social status, as is expected for those people buried in mounds. We do not have a single isotopic datum for the latter. Moreover, due to the practice of cremation it is difficult to obtain isotopic information about them. In the case of the Guarani samples, there are no archaeological data indicating differences of status between individuals. However, this is an almost completely unexplored topic in Guarani archaeology; the use of isotopic analysis would thus represent an excellent way to study this question in the near future. The second consideration is the age of individuals analysed. Juveniles are between 12 and 20 years. Therefore, the isotopic values presented here could be mixed with the diet of the weaning
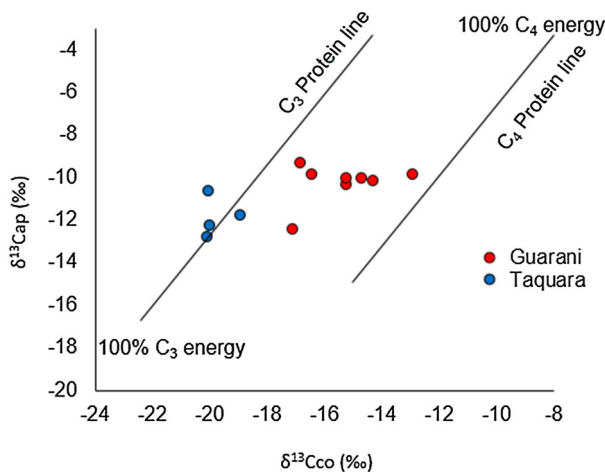

Figure 5 Values of the $\delta^{13}C_{co}$ and $\delta^{13}C_{ap}$ values for humans (Guarani-Taquara) within the linear dietary model for carbon isotopes proposed by Kellner and Schoeninger (2007).
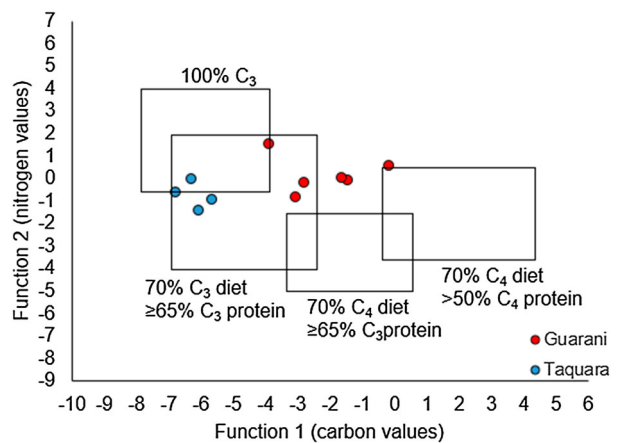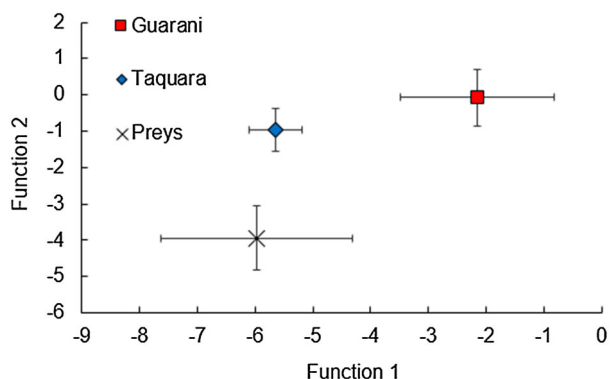

Figure 6 F1 and F2 discriminant function values from individuals recovered from the Taquara and Guarani sites, plotted against previously generated dietary clusters (see Froehle *et al*. 2012).

Figure 7 Discriminant function values of the samples listed in Table 1 (after Froehle *et al.* 2012).

stage. Moreover, we need to include infants (< 3 years) and children (< 12 years) in our future analyses, in order to document a possible enrichment in the $\delta^{13}C$ values due to the intake of soft foods based on maize during the weaning process (i.e. Katzenberg *et al.* 1993; Mansell *et al.* 2006; Slovak and Paytan 2009).

Oxygen

The precipitation in the regions studied here come from two different sources. On the Paraná Basin, they are particularly related to the South American Summer Monsoon (MSSA), associated with the Inter Tropical Convergence Zone (ITCZ), which regulates the amount of precipitation in the tropical and subtropical zones of South America (Gan *et al.* 2004; Vuille *et al.* 2003; Zhou and Lau 1998). These waters flow along the Paraná Basin to its mouth, where the Paraná Delta is located. A recent analysis of the waters in the discharge area of the Paraná Delta provided an average value of $\delta^{18}O$ -4.5 ± 1.3‰ ($\pm 2\sigma$) (analytical error ± 0.1‰) (based on Panarello and Dapeña 2009:107, Table 1). Therefore, the range of $\delta^{18}O$ -5.7‰ / -3.2‰ is expected for the organisms that develop their life cycles in the Paraná River valley, which is defined as the isotopic ecozone 1 (ECZ1). Planalto, like the Paraná Basin, is also affected by monsoon rains, especially during the summer, but during the rest of the year it receives high quantities of extratropical rainfalls due to mid-latitude cyclonic activity over the Atlantic Ocean, whose proximity also provides constant moisture to the air (Cruz *et al.* 2009; Rao *et al.* 1996) (see Fig. 8). The content of $\delta^{18}O$ in this source of water is substantially enriched compared to the monsoon waters (Cruz *et al.* 2005, 2006; Rao *et al.* 1996; Vera *et al.* 2002). This rain falls into the headwaters of the Uruguay River and its watershed, which extends to its mouth. While there is no systematic analysis as the one conducted by Panarello and Dapeña, there are enough records in the Planalto with numerous values below -3‰ (Cruz *et al.* 2005, 2006; pers.
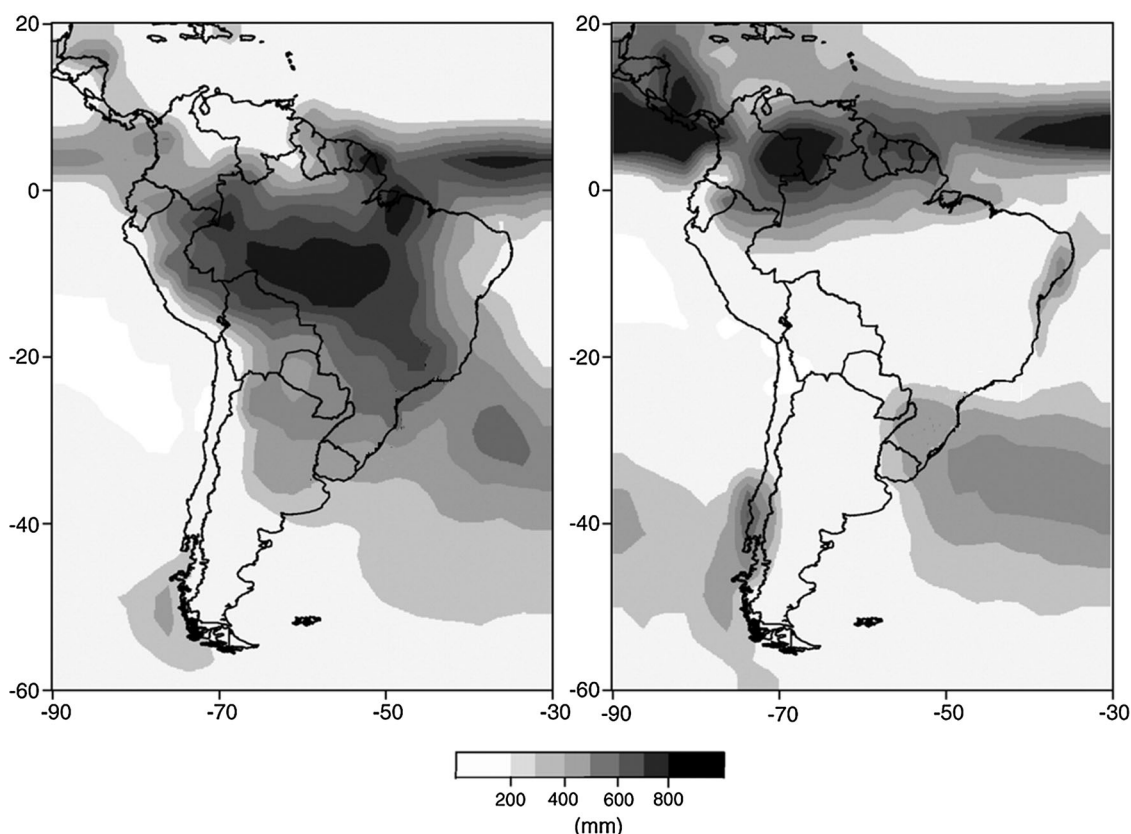

Figure 8 Long term (1979–2000) Climate Prediction Center Merged Analysis of Precipitation. Seasonal precipitation totals for December–February (left) and June–August (right). Taken and modified from Cruz *et al.* (2006).

Table 4 Values of $\delta^{18}O$ in humans and prey

	Sites	Taxon	ID sample	ID Lab.	$\delta^{18}O$	Source
Isotopic ecozone 1	Corpus	*Homo sapiens*	SCE01	EIL-2013	−3.7	(1)
	Corpus	*Homo sapiens*	SCE02	EIL-2014	−3.5	(1)
	Arroyo Malo	*Homo sapiens*	AM 6630/T4-16	AIE 11719/25	−3.9	(1)
	Arroyo Malo	*Homo sapiens*	AM 6631/T5-11	AIE 12365/409	−3.3	(1)
	Arroyo Fredes	*Homo sapiens*	AFR6869	Sirfer 13-2299	−3.3	(1)
	Arroyo Fredes	*Homo sapiens*	AFR6858	Sirfer 13-2300	−3.5	(1)
	Arroyo Fredes	*Homo sapiens*	AFR6856	Sirfer 13-2301	−4.3	(1)
	Arroyo Fredes	*Homo sapiens*	AFR6857	Sirfer 13-2302	−4.7	(1)
	Arroyo Fredes	*Homo sapiens*	AFE-1	EIL-1003	−2.1	(1)
	Arroyo Fredes	*Homo sapiens*	AFE-2	EIL-1004	−2.4	(1)
	LBS1	*Homo sapiens*	LBS1-33	UGA 8780	−3.3	(2)
	LBS2	*Homo sapiens*	LBS2- 12	UGA 8781	−3.9	(2)
	Garín	*Homo sapiens*	G1	UGA 8783	−4.1	(2)
	Garin	*M. coypus*	G227	UGA 9905	−2.8	(2)
	Garin	*Pimelodidae*	G228	UGA 9909	−3.3	(2)
	Anahi	*Doradidae*	A-600	UGA 9906	−3.9	(2)
	Anahi	*B. dichotomus*	A-700	UGA 9907	−3.4	(2)
Isotopic ecozone 2	Saltinho do Uruguay	*Homo sapiens*	1 ACHSU3C2	EIL-2000	−3.1	(1)
	Saltinho do Uruguay	*Homo sapiens*	2 ACHSU3C2	EIL-2001	−1.6	(1)
	Saltinho do Uruguay	*Homo sapiens*	3 ACHSU3C2	EIL-2002	−1.2	(1)
	Saltinho do Uruguay	*Homo sapiens*	4 ACHSU3C2	EIL-2003	−1.7	(1)
	Saltinho do Uruguay	*Homo sapiens*	5 ACHSU3C2	EIL-2004	−1.5	(1)
	Saltinho do Uruguay	*Homo sapiens*	6 ACHSU3C2	EIL-2005	−1.2	(1)
	Abrigo do Matemático	*Homo sapiens*	AM-1	EIL-2007	−1.2	(1)
	Abrigo do Matemático	*Homo sapiens*	AM-2	EIL-2008	−1.4	(1)
	Abrigo do Matemático	*Homo sapiens*	AM-3	EIL-2009	−1.9	(1)
	Abrigo do Matemático	*Homo sapiens*	AM-4	EIL-2010	−1.7	(1)

Sources: (1) This paper. (2) Loponte (2008).

comm. 2015). For this study, we considered it as a second isotope ecozone (ECZ2). In order to increase the number of archaeological samples to compare the isotope values of both ecozones, we have included other pre-Columbian populations of the Paraná Delta (ECZ1) (see Table 4).
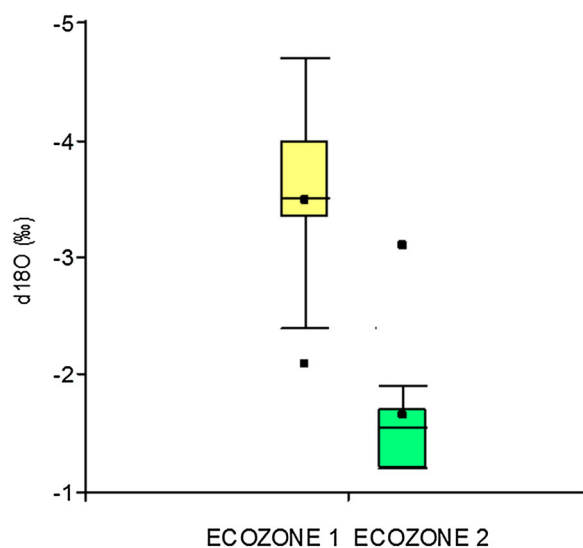
Figure 9 Values of $\delta^{18}O$. The isotopic Ecozone 1 corresponds to the valley of the Paraná River (Paraná Forest + Paraná Delta). The isotopic Ecozone 2 corresponds to Planalto (Araucaria Forest). The outlier of ECZ1 corresponds to the individual AFE-1 (Arroyo Fredes, Paraná Delta). In ECZ2 the outlier corresponds to the individual 1ACHSU3C2 (Saltinho do Uruguay).

The results show significant differences between the two isotopic ecozones ($T = -7.46$; $P < 0.0001$) (Figs. 8 and 9). The ECZ1 groups 17 samples from the Paraná River valley (Paraná Forest + Paraná Delta), with an average of $-3.5 \pm 0.6‰$ (CV = 18.1%), with the 75th percentile at 3.3‰. Within this group, the two individuals AFE-1 and -2 from Arroyo Fredes show some differences from the rest of the samples, with values close to $-2‰$. These individuals also have a spacing of carbon sources significantly different from the rest of the Guarani population (see Table 3). These data suggest that a significant fraction of their life cycles could be developed outside of the ECZ1. These two samples enrich the $\delta^{18}O$ values and make the dispersion in this isotopic ecozone wider; otherwise, its typical range could be restricted to $-3.7 \pm 0.5‰$ (coefficient of variation: CV = 13.5%; confidence interval: CI = -3.83 / -3.16). In ECZ2, the values are quite different. The samples from Saltinho do Uruguai and Abrigo do Matematico have similar magnitudes ($W = 21.5$; $P = 0.961$), showing an average of $-1.5 \pm 0.3‰$ (CV = 16.5%; CI = -1.69 / -1.29, excluding one outlier, see below). While it is clear that Saltinho do Uruguai is located in the Paraná Forest, its landscape is certainly included in the Uruguay Basin, whose headwaters and rainfall are related to the Planalto – Araucarian Forest. However, one individual (1ACHSU3C2) has an outlier value of $\delta^{18}O$ of $-3.08‰$, close to those from the Paraná Valley. We suggest that this is indicative of population movements between these two regions (see Table 4 and Fig. 9).

Figure 10 Isotopic ecozones based on the values of $\delta^{18}O$.

We still need to precisely define the limits of both ecozones, especially related to the ECZ2 to the north (northern Araucaria Forest) and to the south. Some initial results with samples from the middle and lower Uruguay River indicate enriched values comparable with those from ECZ2. At this stage of our research, we can tentatively suggest the existence of rough borders between these two ecozones, as illustrated in Fig. 10, a hypothesis to be tested more thoroughly in the future.

Conclusions

In this work we have characterised two continental diets of horticulturalist groups. While each one is related to a particular archaeological unit, it is more reasonable to think that they are correlated to different ecological areas rather than to cultural units, since, as we have seen, individuals recovered from the 3 de Mayo Cave (Taquara unit, Paraná Forest) show equivalent values to those observed for individuals recovered from the Guarani sites (Paraná Delta + Paraná Forest). This economic organisation, adapted to each particular environment, also has its counterpart at sites located on the Atlantic coast, where the diet is essentially marine (Bastos *et al*. 2014, 2015; Colonese *et al*. 2014; de Masi 2001, 2009). However, we still need a better quality of samples in order to understand if these adaptations are related not only to environments, but also to chronological aspects. In this sense, we have no samples of equivalent age recovered from the Planalto than those available in the Paraná Forest.

In the Planalto, no data support that maize was important in the diet, although reliance on plant foods (C_3) was significant. We do not know if these were cultivated or wild. However, the importance of *A. angustifolia* (C_3) seeds in the archaeological record and in historical sources, make us think that they are responsible for much of the vegetable intake. The C_3 monoisotopic signal of the diet is reinforced by the hunted species, all of them within this photosynthetic pattern. However, one of the individuals recovered here with an enriched diet shows that within the range 1180–1290 years ^{14}C BP there was already a significant consumption of maize in the Planalto or in an adjacent sector, and/or in a part of the population of the region.

On the contrary, the $\delta^{18}O$ values detected in the individuals recovered from the Paraná Forest meet the expectations of a mixed diet that includes a significant intake of maize, but the data indicate that this was not as important as found in other regions in the American lowlands (Froehle *et al*. 2012; Metcalfe *et al*. 2009; Rand *et al*. 2013; Scherer *et al*. 2007; Stronge 2012; Tykot 2002; White *et al*. 2006). The high values of nitrogen also implies an important intake of animal proteins. The negative carbon values of fish could mask a higher maize consumption, as well as the canopy effect, whose impact is still unknown in the area. Regardless, the isotopic values from individuals recovered from the Arroyo Malo and Arroyo Fredes sites (Guarani unit, Paraná Delta) are the strongest evidence regarding the southernmost distribution of the pre-Columbian cultivation of maize in South America, on the Atlantic side, reaching the Río de La Plata River at 34° SL.

The values of $\delta^{18}O$ presented and discussed in this study allow us to identify two isotopic zones for

archaeological purposes. Our results indicate enriched values of oxygen for Planalto individuals and depleted ones for those from the Paraná River Valley. The identification of outliers suggest a significant degree of human mobility between both ecozones, which is consistent with the interaction observed in the archaeological Guarani record (Loponte and Acosta 2013) and the available historical data (Dorantes, in Levillier 1915; Medina 1908).

Further analyses are being conducted with numerous samples from different regions of the Paraná and Uruguay Basins, which should provide in the short term a substantial extension of the isotopic database regarding diet and human mobility in southeastern South America. This study also highlights the benefits of an analytical approach that goes beyond existing international boundaries. This is clear when we are analysing archaeological units and ecozones which are distributed in both countries, which raises an indispensable exchange of ideas and data, and the development of joint agendas of research, of which this work is a small example.

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