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Original Research Article

Spatial Variation of Dental Caries in Late Holocene Samples of Southern South America: A Geostatistical Study

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ABSTRACT: Objective: The spatial variation of dental caries in late Holocene southern South American populations will be analyzed using geostatistical methods. The existence of a continuous geographical pattern of dental caries variation will be tested.

Methods: The author recorded dental caries in 400 individuals, collated this information with published caries data from 666 additional individuals, and calculated a Caries Index. The caries spatial distribution was evaluated by means of 2D maps and scatterplots. Geostatistical analyses were performed by calculating Moran's *I*, correlograms and a Procrustes analysis.

Results: There is a relatively strong latitudinal continuous gradient of dental caries variation, especially in the extremes of the distribution. Moreover, the association between dental caries and geography was relatively high ($m_{12} = 0.6$). Although northern and southern samples had the highest and lowest frequencies of dental caries, respectively, the central ones had the largest variation and had lower rates of caries than expected.

Conclusion: The large variation in frequencies of dental caries in populations located in the center of the distribution could be explained by their subsistence strategies, characterized either by the consumption of wild cariogenic plants or cultigens (obtained locally or by exchange), a reliance on fishing, or the incorporation of plants rich in starch rather than carbohydrates. It is suggested that dental caries must be considered a multifactorial disease which results from the interaction of cultural practices and environmental factors. This can change how we understand subsistence strategies as well as how we interpret dental caries rates. Am. J. Hum. Biol. 28:825–836, 2016.

Dental caries is a common condition that results from an infectious disease process. It is a consequence of the demineralization of dental tissues, due to the production of organic acids from bacterial fermentation (i.e., *Streptococcus mutans*) as a result of the sugar component of the foods consumed (Hillson, 2008; Larsen et al., 1991; Mc Hug, 1970; Ortner and Putschar, 1981). Analysis of dental caries helps to infer the diet of prehistoric populations; an extensive review of the literature on oral health documents the close relation between dental caries and the amount of carbohydrate intake (Larsen et al., 1991; Lukacs, 1992; Turner, 1979). As high-carbohydrate diets are generally associated with higher frequencies of dental caries (Goodman et al., 1984), the percentage of caries expected for hunter-gatherer groups is much lower than that expected among agriculturalists (Cohen and Armelagos, 1984; Larsen, 1987; Larsen et al., 1991; Ortner, 2003; Waldron, 2009). The negative correlation between high degrees of dental wear (DW) and low prevalence of caries, characteristic of hunter-gatherer groups, as well as the positive correlation between high prevalence of dental caries and agricultural economies (characterized by the consumption of soft, sticky food and sugar), have been widely documented (Hillson, 1990, 2008; Larsen et al., 1991; Walker and Erlandson, 1986, among others). As such, dental caries rates have been used as an independent control for subsistence reconstructions, complemented with the analysis of flora, fauna, associated technology (Walker, 1978) and, more recently, carbon stable isotopes (Ambrose, 1986).

Studies of dental caries in prehistoric populations around the world focus mainly on methodological issues related to diagnosis, recording, and calibration (Buikstra and Ubelaker, 1994; Duyar and Erdal, 2003; Hillson, 2001; Lukacs, 1995; Moore and Corbett, 1971), or the description of oral health in samples coming from an archaeological site, locality, or archaeological area (DaGloria and Larsen, 2014; Fujita et al., 2007; Lukacs and Pal, 1993; Lukacs, 2011; Watson et al., 2010). Other studies evaluate temporal variation in the percentage of caries, mainly due to the incorporation of carbohydrates into the diet of the studied populations (Gomez Otero and Novellino, 2011; Larsen, 1995, 2006; Temple and Larsen, 2007; Willis and Oxenham, 2013). However, only a few archaeological studies evaluate variation in the percentage of dental caries among prehistoric populations on a large geographical scale.

In contrast, there are numerous investigations of contemporary populations which focus on spatial variation in dental caries by means of spatial analysis and GIS studies. In general, those studies interpret spatial variation in the percentage of dental caries as manifestations of socioeconomic differences and differences in the degree of access to a health system (Almado et al., 2013; Chattopadhyay, 2008; Ferreira Antunes et al., 2003, 2004; Strömberg et al., 2011). Although some studies analyze variation in dental caries in prehistoric populations in large regions (i.e., comparing samples that come from different archaeological sites; Littleton and Frohlich, 1993; Sealy et al., 1992), those studies do not adopt

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geostatistical approaches. Moreover, there are studies that use geostatistical analysis to examine the distribution of dental caries, but they do not analyze the distribution in a geographical region. Instead, they focus on the spatial distribution of dental caries among neighboring teeth within an individual (Bandyopadhyay et al., 2009).

Geostatistical analyses provide tools to evaluate the patterns and spatial structure of an ecological or biological variable across geographical space (Fortin and Dale, 2005). The description of spatial structures in data can help us improve our understanding of populations, species, and community distributions (Legendre, 1993) because biological data are usually characterized by spatial autocorrelation (Fortin et al., 2002). Spatial autocorrelation occurs when samples closer in a geographical space tend to be more similar or dissimilar than what it is expected randomly for a given variable (Legendre and Legendre, 2003). Thus, the existence of a spatial structure in the sample implies that any phenomenon, located at a given spatial point, may have an influence on other points located close by, or even at a certain short distance. The advantage of spatial analysis is that spatial autocorrelation is incorporated into the statistical test among the predictors of the model (Diniz-Filho et al., 2009; Legendre, 1993), allowing for testing and describing the presence of a spatial structure in a particular geographical region (Legendre and Fortin, 1989). A geostatistical approach to dental caries studies yields an evaluation of the spatial pattern and spatial structure of caries variation in a large geographical area. With geostatistical analysis, frequencies of dental caries can be analyzed as one of the variables which comprise an ecological niche (Hutchinson, 1957), particularly related to diet composition (Menéndez, 2015).

Southern South America is a region of great interest for understanding subsistence and dental caries patterns because it was one of the last regions of the world to be colonized by modern humans (ca., 12,500–13,000 BP; Borrero, 1999; Lanata et al., 2008; Menéndez et al., 2015; Neves and Hubbe, 2005), and is characterized by a wide range of environments with large differences in mean annual temperature (from 21° to 4°)—and consequently in available resources—spread along 3,500 km. This ecological variation has increased during the last 3,000 years (during the late Holocene) because of food production practices (i.e., agriculture and pastoralism) and technologies (i.e., pottery and grinding tools). So, during the late Holocene, southern South America was characterized by major variation in subsistence strategies (Harlan, 1971; Pearsall, 2008). Such variation presents a continuous north-to-south gradient in the geographical space of southern South America, which ranges from southern hunter-gatherers, focused on marine (shellfishes, fishes, mammals) or terrestrial (mammals, birds, fruits) resources (Scheinsohn, 2003), to northern pastoralist (camelids), and agricultural groups, which domesticated several plants (maize, potato, manioc, and bean) (Gasco, 2014; Killian Galván et al., 2012; Mazoyer and Roudart, 2006; Piperno and Pearsall, 1998), as well as a mixture of subsistence strategies that combined all of the above in different proportions. Additionally, some horticultural groups inhabited the center of the spatial distribution (Azul).

One way of differentiating among subsistence strategies in the late Holocene populations of southern South America could be through the wider availability of carbohydrates related to horticultural and agricultural practices, when compared with the larger proportion of proteins consumed by hunter-gatherer groups (Harlan, 1971; Pearsall, 2008; Perez et al., 2011; see Table 1). Subsistence strategies of the populations that inhabited southern South America are a widely studied topic, which have been examined through zooarchaeological and archaeobotanical remains, isotopic analyses, and bioarchaeological indicators—such as dental caries. Since the mid-twentieth century, various researchers have also been interested in the study of dental caries in human populations inhabiting different archaeological sites and areas of southern South America (Aranda et al., 2012; Baffi et al., 1996; Bárcena, 1974–1976; Bernal et al., 2007; Fabra et al., 2012; Flensborg, 2011; García Guraieb, 2010; Gheggi, 2012; Gomez Otero and Novellino, 2011; Guichon and Suby, 2011; Kozameh and Barbosa, 1992, 1996; L'Heureux, 2000; Mazza and Barrientos, 2012; Menéndez, 2010; Merlo et al., 2005; Miranda, 2012; Piccoli, 2009; Seldes, 2012).

The goal of this study was to study the spatial variation in dental caries in populations which inhabited southern South America during the late Holocene (last 3,000 years BP). To achieve this, data on dental caries were collected and further information was obtained from previously published papers. Data were analyzed using geostatistical analysis. This specific analysis allows for the incorporation of spatial autocorrelation in the statistical test, so as to evaluate the spatial pattern and structure of variation of dental caries. Given the association between caries and the degree of carbohydrates intake, a geographical continuous gradient for the percentages of dental caries was expected: with the northern populations having the highest rates and the southern samples showing lower rates. This is consistent with the subsistence strategies suggested by the archaeological record, where the proportion of carbohydrates in the diet decreases southwards. Conversely, if results show that there is no continuum in the frequency of dental caries, then a more complex scenario could be posited, in which some of these groups could be obtaining carbohydrates from sources other than domesticated plants, and/or dental caries may be the product of other components in the diet of the studied populations.

MATERIALS AND METHODS

Studied archaeological samples

The presence or absence of caries was recorded in 11,569 teeth belonging to 1,066 individuals (Table 1). Samples included skulls from late Holocene archaeological sites (3,000–400 years BP) from different geographical regions (Fig. 1) that correspond to the north (North-West [NW], Central Highlands [CH]), center (Central-West [CW], Paraná Delta [D], Pampa [PA]), and south (North Patagonia [NP], Central Patagonia [CP], and South Patagonia [SP]) of the study area. A total of 29 samples corresponding to different archaeological sites were studied. Data were collected by the present author ($N = 400$), but most of the information was collated from available published material ($N = 666$) (see Table 1 for details).

Adults of both sexes were included in the present study. The majority of individuals were represented only by skulls, with age and sex determinations restricted to cranial traits (Buikstra and Ubelaker, 1994). Generally, equal numbers of males and females were available

TABLE 1. Detailed data on the archaeological samples included in the present study organized by geographical region (and its abbreviation), chronological period, sample abbreviation, archaeological site (and its Province), diet[a], Caries Index (CI), number of individuals studied (Ni), number of teeth registered (Nt), number of caries (Nc), chronology (radiocarbon dates as years BP), bibliographical reference of CI data, and museum that hosts the sample [ME= Museo Etnográfico (Buenos Aires); MLP = Museo de La Plata (La Plata); MG= Instituto de Investigaciones Arqueológicas y Museo "Prof. M. Gambier" (San Juan); MJCM= Museo de Ciencias Naturales y Antropológicas "J.C. Moyano" (Mendoza); MSR = Museo de Historia Natural de San Rafael (San Rafael); MM = Museo Regional de Malargüe (Malargüe); MAC= Museo de Antropología (Córdoba); MHMLP= Museo Histórico Municipal (La Para), MAAM= Museo Aníbal Montes (Miramar); MAPAM= Museo Arqueológico Provincial Aníbal Montes (Rio Segundo); MEP= Museo Estrella de Piedra (Valle Rumipal); MHAPG= Museo Histórico Arqueológico (Potrero de Garay); INCUAPA= Núcleo Consolidado de Investigaciones Arqueológicas y Paleontológicas del Cuaternario Pampeano (Olavarría); INAPL= Instituto Nacional de Antropología y Pensamiento Latinoamericano (Buenos Aires); CENPAT= Centro Nacional Patagónico (Puerto Madryn); CADIC = Centro Austral de Investigaciones Científicas (Ushuaia)]

Geographical Region	Chronological period	Sample Abbreviation	Archaeological Site (Province)	Diet[a]	CI	Ni	Nt	Nc	Chronology	Bibliographic reference of CI	Host
Northwest (NW)	Final late Holocene	Am	Amarillos (Jujuy)	1	15.00	28	140	21	700 ± 60	Menéndez et al. 2014a	ME
		Don	Doncellas (Jujuy)	1	10.63	14	94	10	700 ± 60	Miranda 2012	ME
		Til	Tilcara (Jujuy)	1	12.18	54	985	120	910 ± 50	Menéndez et al. 2014a	ME
		Pom	La Poma (Salta)	1	11.95	49	569	68	821 ± 40	Menéndez et al. 2014a	ME
		Pg	Pampa Grande (Salta)	1	13.69	13	168	23	1310 ± 40	This work	MLP
		And	Andalgala (Catamarca)	1	13.45	22	229	30	400 ± 50	Menéndez et al. 2014a	MLP
Central Highlands (CH)	Final late Holocene	Co1	Córdoba 1 (Córdoba)	2	10.24	28	566	58	1500– 383 ± 58	Fabra et al. 2012	MAC-MHMLP-MAAM-MAPAM-MEP-MHAPG
	Early late Holocene	Co2	Córdoba 2 (Córdoba)	2	9.48	7	116	11	2707 ± 61–1500	Fabra et al. 2012	MAC-MHMLP-MAAM-MAPAM-MEP-MHAPG
Central-West (CW)	Final late Holocene	Nsj	North San Juan (San Juan)	1	3.28	25	304	10	559 ± 40	Menéndez 2015	MG-MLP
		Ssj	South San Juan (San Juan)	1	13.18	18	182	24	1080 ± 45	Menéndez 2015	MLP-ME
		Nmz	North Mendoza (Mendoza)	1	4.67	82	1154	54	1080 ± 45	Menéndez et al. 2014b	MJCM-ME
		Smz	South Mendoza (Mendoza)	3	3.97	57	579	23	1766 ± 50	Menéndez et al. 2014a	MSR-MM-ME
Paraná Delta (D)	Final late Holocene	Par	Paraná river (Entre Ríos)	3	0.96	252	1874	18	1800–500	Mazza and Barrientos 2012	MLP-INAPL-ME
	Final late Holocene	A	Azul (Buenos Aires)	2	7.55	38	397	30	1300 ± 40	Menéndez et al. 2014a	MLP
Pampa (PA)		Se1	Southeast Pampa 1 (Buenos Aires)	2	3.44	12	232	8	2000–400	ĹHeureux 2000	MLP-INCUAPA
	Early late Holocene	Se2	Southeast Pampa 2 (Buenos Aires)	2	18.80	13	202	38	3000–2000	ĹHeureux 2000	MLP-INCUAPA
North Patagonia (NP)	Final late Holocene	Pa1	Paso Alsina 1 (Buenos Aires)	3	5.76	51	781	45	483 ± 20	Flensborg 2011	INCUAPA
		Nv	Negro river valley (Rio Negro)	3	0.89	30	223	2	523 ± 45	Bernal et al. 2007	MLP
		Sb	San Blas (Buenos Aires)	3	1.03	46	388	4	1028 ± 45	Bernal et al. 2007	MLP
	Early late Holocene	Smf	San Matias Gulf (Rio Negro)	3	1.90	4	105	2	2300	García Guraieb et al. 2010	INCUAPA
		Lm	Loma de los Muertos (Rio Negro)	3	11.76	3	34	4	2088–3027 ± 47	Prates et al. 2010	INCUAPA
		Lj	Laguna del Juncal (Rio Negro)	3	0.95	32	210	2	4000–2500	Bernal et al. 2007	ME
Central Patagonia (CP)	Final late Holocene	Sc1	Sierra Colorada 1 (Santa Cruz)	3	9.45	6	148	14	800–350	Gomez Otero y Novellino 2011	CENPAT
		Chs1	Chubut seashore 1 (Chubut)	3	3.58	24	307	11	1050–400 ± 50	Gomez Otero and Novellino 2011	CENPAT
		Chv	Chubut valley (Chubut)	3	3.53	74	989	35	1326 ± 65	Bernal et al. 2007	MLP
	Early late Holocene	Sc2	Sierra Colorada 2 (Santa Cruz)	3	2.58	8	116	3	2600–1200	García Guraieb 2010	INAPL
		Chs2	Chubut seashore 2 (Chubut)	3	0.71	8	140	1	2600–1400 ± 60	García Guraieb 2010	INAPL
South Patagonia (SP)	Final late Holocene	Tf	Tierra del Fuego (Tierra del Fuego)	3	2.23	19	268	6	850	Schinder and Guichon 2003	CADIC
		Cf	Caleta Falsa (Tierra del Fuego)	3	2.89	4	69	2	820 ± 40	Guichon and Suby 2011	CADIC
Totals						1021	11569	677			

[a]Samples were classified, following Perez et al., (2011), based on the proportion of carbohydrates and proteins on their diet: (1) Rich in carbohydrates; (2) Mainly terrestrial proteins with a complement of carbohydrates; (3) Rich in proteins. Abbreviations are indicated in capital letters for regions.

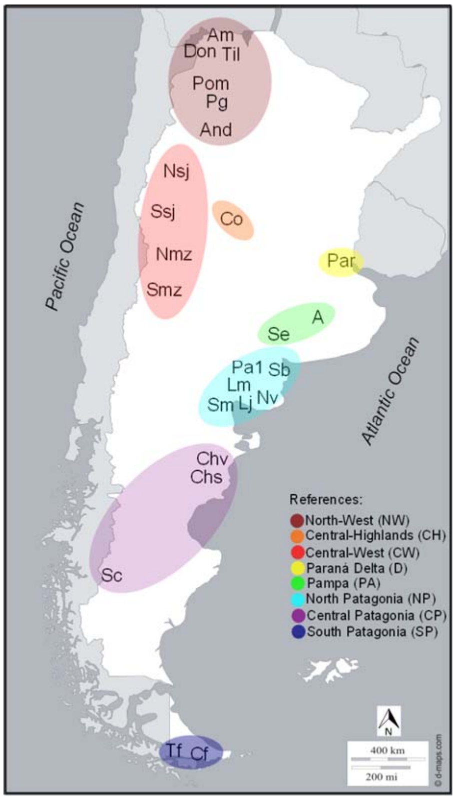

Fig. 1. Distribution of the archaeological samples (Abbreviations correspond to those in Table 1) included in the present study, grouped by geographical region as indicated in the references on the right. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

because sex differences in dental caries frequencies were reported previously (Ferraro and Vieira, 2010; Lukacs and Largaespada, 2006; Temple, 2011). Subadults and elderly individuals were excluded from the analysis to avoid introducing differences in the degree of dental caries due to age variation. Therefore, individuals were assigned to one of two categories: subadult and adult. Adults were classified as those who had an erupted third molar and a closed sphenobasilar suture. Moreover, individuals with malformations, pathologies, several antemortem tooth losses (ATL), or high DW were excluded from this study. Because we considered that ATL affected the results of the frequencies of dental caries, we decided to exclude samples with more than three ATL. With respect to DW, a test—described below—was carried out to analyze whether it influenced the count of frequencies of dental caries.

Environmental variation in each geographical region was taken into account because of differences in available dietary resources. The sampled groups inhabited different geographical and ecological regions (Table 1), ranging from 22°S latitude to 54°S latitude (Fig. 1). According to existing subsistence categories, the studied samples were comprised of groups with agricultural economies, horticulturalists with a small-scale and highly diversified cultivation system, pastoralists, and terrestrial and maritime hunter-gatherers (Berberián and Nielsen, 2001). However, given that some samples may have combined some of these subsistence strategies, they were grouped according to their dietary components (carbohydrates of domesticated plants versus proteins of terrestrial mammals or marine mollusks, or a balanced combination of both) following Larsen (2006), as Table 1 shows. A diet was classified as "rich" in a given component when such component was available and consumed all year round, rather than seasonally. According to archaeological evidence, the northern groups, NW and "Córdoba" in the CH, may have had a diet rich in carbohydrates (Olivera, 2001), except for "Doncellas," "North San Juan," and "South San Juan," that may show a considerable consumption of proteins as a result of pastoralism (Gasco, 2014; Killian Galván et al., 2012). The Southern groups' samples —CP and SP— had a diet rich in terrestrial mammal and/or marine mollusk proteins (Scheinsohn, 2003). The intermediate groups had a mixed diet that combined a great diversity of subsistence strategies. While some of the latter groups were considered horticulturists ("Azul" and "Paraná River" from PA and D; Bonomo et al., 2011; Silva Diaz, 2014), others incorporated domesticated plants into their diet, although they did not cultivate them, and were defined as having a mixed diet ("North Mendoza," "South Mendoza" from CW, most of NP samples, and "Southeast" from PA; Menéndez, 2015; Neme and Gil, 2013).

Considering that the type of diet varied in relation to both the available resources and cultural practices, samples were grouped into three classification schemes. The first classification was designed according to the geographical region; the second one by chronological period, whereby samples were separated into final late Holocene ($N = 22$; 2,000–400 years BP) and early late Holocene ($N = 7$; 3,000–2,000 years BP); and the third one according to the archaeological site which corresponded to local populations (Table 1). Given the difficulty of recognizing populations in the archaeological record, the concept of population employed here was based on spatiotemporal criteria, where individuals who inhabited a geographical area for a limited period of time belonged to different local populations (Bernal, 2008; Cavalli-Sforza et al., 1994; Menéndez, 2015). The geographical coordinates of each local population were transformed to a geodesic system (decimal degrees of latitude and longitude) and used to compute a matrix of great circle geographical distances between population pairs (geodesic distances expressed in kilometers).

Collection of dental caries data and caries index calculation

There is broad consensus among researchers regarding the definition of dental caries as points or regions of dark coloration and eroded surfaces found on enamel, dentin, and even on dental roots (Hillson, 2008; Larsen, 1987; Larsen et al., 1991; Lenander-Lumikari and Loimaranta, 2000; Mc Hug, 1970). The presence of those dark and eroded tooth surfaces in the occlusal and interproximal surfaces of the teeth, as well as on exposed roots, was examined with the help of a dental explorer. The dental caries data collected from the literature were identified with the same criteria. Finally, a Caries Index (CI) was calculated as a function of the number of cariogenic teeth and the total number of available teeth for each sample. Many researchers have criticized the CI for not being informative enough, due to a lack of data about the potential presence of dental caries in teeth that were absent due to antemortem or postmortem loss. There are various alternative methods of correction presented by Hillson (2001). However, in the present work, the CI was applied for three main reasons: (a) it is most frequently reported in the literature; (b) it is the simplest index to calculate and interpret, with only two types of data usually available, the total number of teeth and caries; and (c) it provides information about the prevalence of caries in a sample, an approximation of frequencies of dental caries in the studied population. CI allowed the comparison of a vast number of samples. The available samples of previous works quantified the total number of teeth and the total number of dental caries in the sample.

As previously mentioned, the prevalence of caries in a sample could be affected by the degree of DW, which is considered a continuous long-lasting process that results from contact between opposite crowns, as well as contact with food or abrasive materials (Smith, 1984). DW might remove both fissures of erupting molars before they became carious, as well as the carious tissue, as soon as the lesion appears (Hillson, 2000). For that reason, in a previous study which included most of the samples analyzed here (Menéndez et al., 2014a), DW was recorded to get an indirect control of the quantification of carious lesions. A principal axis analysis was applied to estimate the rates of dental caries between M1 and M2, and the slope obtained was then used as an indicator of the relationship between adjacent molars and DW rate (Scott and Turner, 1988). Subsequently, DW and dental caries were explored using correlation analyses. The results showed two axes of independent variation given by dental caries and DW, which meant that carious lesions were not related to DW among the samples studied here ($r^2 = 0.28$).

Statistical analyses

Geostatistical analyses were carried out to compare the geographical distribution of dental caries. Spatial structure can arise from various sources such as error measurement, including effects of continuous spatial heterogeneity, and space-dependent mechanisms (Fortin et al., 2002). The subsequent structure of correlation or covariation can be evaluated and used to increase the accuracy of modeling and prediction. Particularly, geostatistical analysis allows us to consider spatial and temporal autocorrelation, which presents a problem for statistical testing (Legendre, 1993). However, spatially autocorrelated datasets present an opportunity to understand the causes of spatial structure in ecological studies (Diniz-Filho et al., 2003; Legendre, 1993). Thus, geostatistical analysis allows for the evaluation of frequencies of caries distribution in a region, without letting proximity between populations influence the results. The resulting diet variation is a product of each population variation.

The spatial distribution of dental caries was evaluated by means of boxplots, 2D maps, and scatterplots. These plots allowed us to describe the presence or absence of an autocorrelation pattern of CI values. Boxplots included all late Holocene samples to show the amplitude of CI variation in that period for all of the regions studied. Two dimensional maps allow the spatial distribution of a variable, and its continuity/discontinuity, to be evaluated. These were obtained using the original data matrices with the decimal geographical coordinates (latitude and longitude) and the CI. They also included a color gradation scale, which represents the rates acquired by the variable of interest. Scatterplots were used to illustrate the relation between the CI and geographical coordinates to see if there was a linear association between a geographical axis and CI. Both 2D maps and scatterplots were done using final late Holocene samples to avoid introducing variation resulting from temporal differences of the groups. These were made using SAM Macroecology software (Rangel et al., 2010), while the boxplots were done with R (Team RC, 2012).

Spatial analysis of dental caries was performed through a Moran's I correlogram and a Procrustes analysis. These analyses together allow the magnitude and direction of autocorrelation of CI values to be evaluated. As with the 2D map and scatterplots, only final late Holocene samples were used for these analyses. Moran's I was calculated and a correlogram was performed to assess whether the distribution of dental caries presented a spatial pattern. Moran's I is a statistical test of spatial autocorrelation (Cliff and Ord, 1981) that behaves mainly as the Pearson correlation coefficient; positive autocorrelation is indicated by positive values, negative autocorrelation by negative values, and the expected value for the absence of spatial autocorrelation is close to 0 (Dale and Fortin, 2014). Rather than taking the difference between a sample value and its mean, as is done in classical variance or correlation functions, spatial functions take the difference in values between all pairs of samples located at a given distance class. Following this, spatial autocorrelation is quantified through pairs of sampled locations that are pooled into different distance classes, which are defined by the researcher or calculated by the software. Plotting the level of spatial autocorrelation against the distance class generates a correlogram that describes quantitatively the geographical pattern of variation and tests for its departure from spatial randomness (Jobling et al., 2004). Each point in a correlogram represents the correlation for all pairs of points within a distance interval. Finally, the shape of the autocorrelation function indicates the type of spatial structure of the data that are being analyzed (Sokal, 1979). The number of distances classes ($n = 8$) was calculated by the software, based on the input of geodesic data (decimal degrees of latitude and longitude) which allowed for the creation of distance units, which are expressed in kilometers. Moran's I and correlograms were also calculated using SAM Macroecology (Rangel et al., 2010).

The association between CI and the geographical space was examined through a PROTEST (Jackson, 1995). The PROTEST is a multivariate ordination technique that combines Procrustes transformation (Gower, 1975) with permutation tests. It uses a rotational-fit algorithm to maximize the sum-of-square distances between corresponding points of two data matrices. Procrustes analysis fits one matrix to another by rotating, translating, and rescaling one matrix to minimize the sum-of-squared residuals between them. The goodness of fit measure between these matrices is the m_2 sum-of squared deviation statistic, which allows evaluating the concordance between the two matrices (Gower, 1975). The goodness of fit (m_{12}), ranges between 0 and 1, the latter identifies the optimum overlap that can be used as a concordance metric (Jackson, 1995). The results and significance coincide with a Pearson correlation. A permutation procedure (9999 permutations) was used to assess the statistical

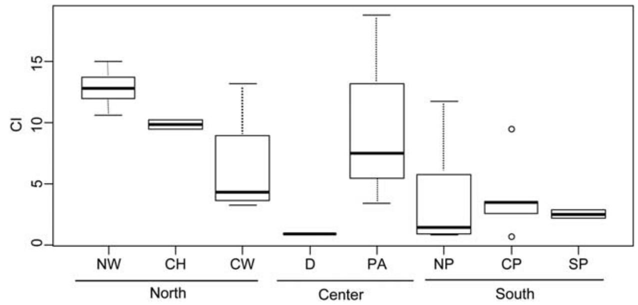

Fig. 2. Boxplots showing the dental caries range in variation through the geographical regions studied. All late Holocene samples are included. In the in the vertical axis CI values are shown, in the horizontal axis the geographical grouping (NW = Northwest; CH = Central Highlands; CW = Central-West; D = Parana Delta; PA = Pampa; NP = North Patagonia; CP = Central Patagonia; SP = South Patagonia).

significance of the Procrustean fit between CI and geographical coordinates (Peres-Neto and Jackson, 2001). This analysis was carried out using the package VEGAN (Oksanen et al., 2010) for R 3.2.1 (Team RC, 2012).

RESULTS

Spatial distribution of dental caries

Boxplots show the range of variation in dental caries in samples of southern South America (Fig. 2). Boxplots were done with all of the samples included in Table 1, both early and final late Holocene. The boxplots indicated that rates of dental caries increased with the latitude. While samples from the north show an increase in CI values with latitude, samples from the center are more diverse, and in general all southern samples show low CI values. The sample that presented the highest rates of dental caries was NW, the most northern sample of the distribution. However, the sample that presented the lowest value was NP, and not SP, as would be expected. While regional samples of the extreme north (NW) and extreme south (SP) of the distribution showed the smallest range of variation (NW/CH vs. CP/SP), as can be seen by the smaller size of the boxes, samples from the center of the distribution (CW, PA, NP) showed the largest range of variation. This confirms that populations from the extremes of the distribution may have had a diet with little variation, characterized by specialization. Conversely, populations of the center of the distribution had a widely varied diet. Some of them may have had a diet based on foods responsible for originating dental caries (A, Lm), while others had lower frequencies (Nv, Par). The CW sample had a large range of variation in rates of dental caries, although on average it had lower rates than expected for that region, which constituted the southern boundary of Pre-Columbian agriculture. Finally, the PA sample presents the widest variation in CI, but its CI values are much higher than what would be expected for horticulturalist groups in the central region.

A 2D map was designed based on the data matrices of the decimal geographical coordinates and CI of final late Holocene samples (Fig. 3). The map showed a geographical gradient of the frequencies of dental caries distributed along the geographical space. In general, the highest rates of CI were located in the north (Am, Pg, And), the lowest

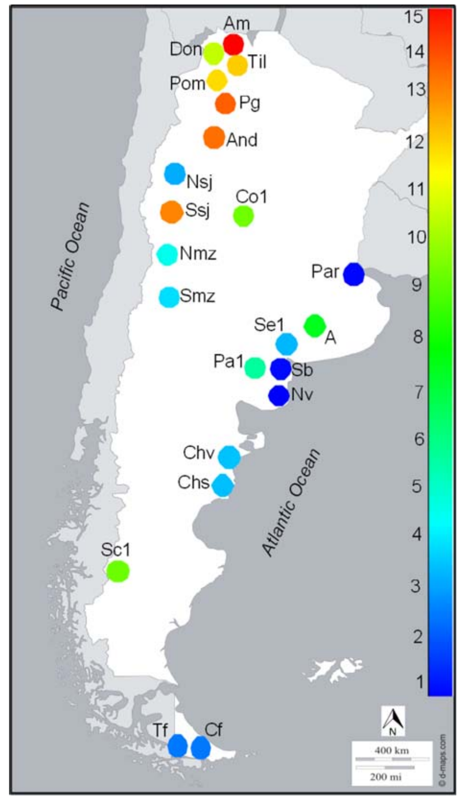

Fig. 3. Two-dimensional map showing the CI variation along southern South America samples. The colored scale in the right indicates the dental caries range of variation (CI). Only final late Holocene samples are included. Abbreviations correspond to the following references [North-West samples (Am: Amarillos, Don: Doncellas, Til: Tilcara, Pom: La Poma, Pg: Pampa Grande, And: Andalgalà), Central Highlands (Cordoba 1), Central-West (Nsj: North San Juan, Ssj: South San Juan, Nmz: North Mendoza, Smz: South Mendoza), Paranà Delta (Par: Paranà river), Pampa (A: Azul, Se1: Southeast Pampa 1), North Patagonia (Pa1: Paso Alsina 1, Nv: Negro river valley, Sb: San Blas), Central Patagonia (Sc1: Sierra Colorada 1, Chs1: Chubut seashore 1, Chv: Chbut valley), South Patagonia (Tf: Tierra del Fuego, Cf: Caleta Falsa)]. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

rates were located in the center (Par) and the north of the south (Nv, Sb), and not the extreme south, as expected. Nonetheless, there were regions (PA, NP, CP, and CW) which did not follow this geographical pattern. In CP, Sc1 sample showed a higher CI value than expected, as well as Pa1 in NP. Conversely, Nv and Sb had lower values than expected for that area. Except for Ssj, the other samples of CW had low rates of CI. This meant that these intermediate regions (CW, PA, NP, D) had lower rates than what it was expected for these areas, although they also had a large variation of CI values.

When variation according to longitude was considered, the results differed for the west and east of the distribution. A stronger geographical continuity in CI could be seen along the west side of the distribution, which coincided with the highlands of the Andes Mountains; except for the CW, which showed low rates of CI. In contrast, when the eastern side of the distribution was taken into account, rates of dental caries showed a random variation, with the lowest rates in the northern extreme (Par) and center (Sb, Nv), intermediate rates in the center (A, Se)

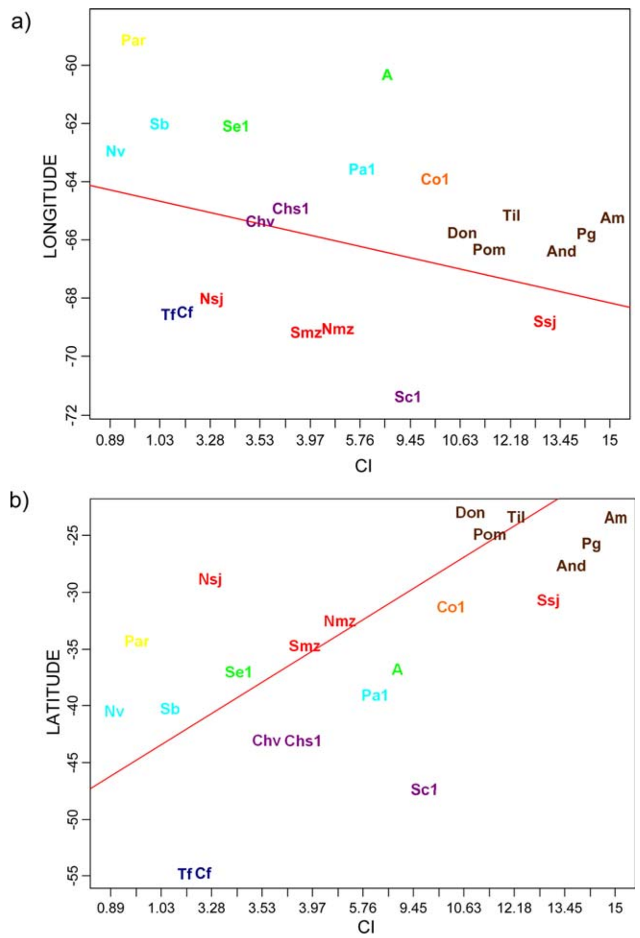

Fig. 4. Scatterplots showing the association of CI with decimal geographical coordinates: a) Longitude, and b) Latitude. Samples colored according to geographical region (Northwest = brown, Central Highlands = orange, Central-West = red, Paranà Delta = yellow, Pampa = -light green, North Patagonia = light blue, Central Patagonia = violet, South Patagonia = blue). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

and in the southern extreme (Chv, Chs1). Therefore, from what we noted in the analysis of the 2D map, it seems that there was a weak spatial structure of variation in CI values of southern South America. While some regions showed wider variations in rates of dental caries (PA, CW, NP, CP), others showed narrower rates of dental caries (NW).

The association between CI and the decimal geographical coordinates was evaluated by means of scatterplots (Fig. 4). As Figure 4 shows, the association was stronger for variation in latitude than longitude, although this association was weak overall ($r^2 = 0.44$). There was no association between CI and longitude ($r^2 = 0.08$), although it appears that northern and western samples had the highest rates of dental caries, while southern and eastern samples had the lowest rates of dental caries. These results confirmed the interpretation of the 2D map, where there was a geographical gradient of CI rates in the west side of the distribution, which covered the total geographical range of the sample, and where there was generally a variation in dental caries rates that could be associated with variations in latitude.

TABLE 2. Moran's I values and significance sorted by distance classes

Distance class	Count	Distance center	Moran's *I*	Standard error	*P*
1	52	192.193	**0.796**	0.169	0.001
2	50	496.191	**0.299**	0.164	0.033
3	50	753.450	0.222	0.170	0.990
4	52	970.354	−0.005	0.155	1.232
5	50	1211.971	−0.339	0.174	1.048
6	50	1479.569	−0.385	0.157	1.176
7	50	1830.362	−0.774	0.162	1.435
8	52	2793.104	−0.317	0.153	0.811

(Significant values in bold) [Distance class: calculated arbitrarily by the software; Count, pairing of cells that are closest together and let define that distance class; Distance center, represents the middle values of a distance class and are expressed in kilometers; Moran's *I*, statistic of correlation; Standard Error, of the statistic; P, significance of Moran's *I*].

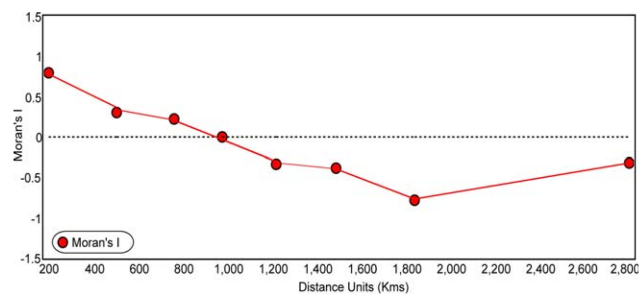

Fig. 5. Spatial correlogram of CI. *Y* axis shows Moran's *I* values; *X* axis shows Distance Units (kilometers). Each red circle represents the average value of autocorrelation observed within each distance class. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Spatial analysis of dental caries

All spatial analyses were done with final late Holocene samples. The spatial analysis of dental caries was evaluated with Moran's *I* statistic (Table 2) and the spatial correlogram was performed with those values (Fig. 5). As expected, Moran's *I* values decreases when the geographical distance among the samples increases (Table 2), which means that samples that were geographically near were more similar to each other than distant samples. Moran's *I* values were significant only for the two first distance classes of the distribution. A high and significant autocorrelation can be observed in the first distance class (Moran's $I = 0.796^{**}$), with samples located at an average distance of 192 km positively autocorrelated. So, we would expect to find similar values of CI among samples located at 192 km of each other. In the distance class 7, Moran's *I* shows a negative autocorrelation (−0.774) which, although not significant, indicates that at a mean of 1,830 km samples are substantially different among each other. The highest and lowest values of the statistic were 0.796 and −0.774, the higher values expected for greater differences among samples for rates of dental caries.

The spatial correlogram (Fig. 5) shows a slight decline in Moran's *I* values, starting near 0.8 (strong positive autocorrelation) and ending near −0.8 (strong negative autocorrelation). This monotonic decrease in Moran's *I* coefficient with respect to geographical distance suggests a clinal pattern in the spatial distribution of CI. This indicates a strong CI similarity among samples of small geographical scales, and greater differences among samples of larger spatial scales. Spatial autocorrelation was strong, which implies that most similarities and differences among near and/or distant samples could be explained by the geographic pattern mentioned above, in which northern and western samples have higher CI values than southern and eastern samples, although there are some exceptions, mainly in the center of the distribution.

Finally, a Procrustes analysis was performed to evaluate the magnitude of association between dental caries variation and geographical space. According to the preceding results, the statistic m_{12} provides a relatively high and significant value ($m_{12} = 0.602$; $P = 0.001$). This means that there is a relatively strong association between dental caries rates and geographical coordinates, suggesting a strong geographical pattern, which agrees with the Moran's I and correlogram results.

DISCUSSION

The results obtained in the present study show a relatively strong association between dental caries of late Holocene human populations of southern South America and geographical space. In general terms, this geographical pattern is characterized by a positive autocorrelation at short distances (i.e., significant similarities of CI among populations living at a geographic distance of up to 200 km) coupled with negative autocorrelation values at large distances (i.e., CI starts to differ among populations separated by 1,800 km). The fact that the western samples have a more continuous pattern of dental caries variation than the eastern samples strengthens the latitudinal rather than longitudinal pattern of CI variation—mainly along the Andes which constituted the axis of plant domestication.

The existence of a spatial pattern among Argentinian prehistoric populations has also been demonstrated in craniofacial studies (Menéndez et al., 2014a), which demonstrate that the geographical distance between local populations is associated with the morphometric distance between them, and that such variation could be explained by differences in diet composition, that is, the degree of carbohydrates and proteins consumed. On a broader scale, other craniofacial studies agree with the existence of a spatial variation in South America (Perez et al., 2007, 2011; Pucciarelli et al., 2006; Varela et al., 2008). Several molecular studies have also demonstrated the existence of spatial structuring among South American populations (Fuselli et al., 2003; Moraga et al., 2000). The spatial pattern found on morphometric studies showed that close populations were more similar to each other than randomly expected (Ives and Zhu, 2006; Legendre, 1993; Perez et al., 2010), meaning that environmental factors, such as diet composition, contribute to the explanation of craniofacial variation (Menéndez et al., 2014a; Perez and Monteiro, 2009; Perez et al., 2011).

Furthermore, the association between CI and geography found in the present study indicates that there is a certain geographical continuous gradient in frequencies of dental caries along the studied region, which is mainly found in the geographical extremes. Northern samples show the highest rates of dental caries, while southern samples show the lowest rates. In agreement with archaeological record expectations, this would mean that the northern groups have the highest rates of dental caries, associated with a diet rich in carbohydrates, while the southern groups would have the lowest dental caries rates, explained by a diet rich in proteins. The results obtained in the south and north of the distribution confirm the hypothesis tested in this study. Beyond methodological differences, this pattern is consistent with the results of an earlier study, which evaluates the spatial variation in dental caries in populations with four types of subsistence along the Arabian Gulf (Littleton and Frohlich, 1993). The authors account for such variation by differences in the intake of carbohydrates in the diet, according to the type of subsistence strategy: while agriculturalists had the highest rates of dental caries, samples with a mixed diet had intermediate rates of dental caries, and samples with a marine subsistence had the lowest rates of dental caries. So, in both studies, in southern South America and in the Arabian Gulf, results seem to describe a geographical continuity of variations in dental caries in relation to the percentage of the intake of carbohydrates.

However, the results show that the geographical pattern found was not as strong as expected, especially in the central area. When we look at the samples of the intermediate area of southern South America (CW, PA, NP, D), rates of dental caries seem to vary randomly, and the samples located in the center of the distribution show the greatest variation in rates of dental caries. Moreover, instead of the expected intermediate values, those samples present lower rates of dental caries than the ones expected for that area. Possible explanations for this discontinuity in dental caries rates are related to different cultural practices that coexisted in that area. All of those populations have a mixed subsistence strategy, which is a broad category that includes large variation and diverse subsistence patterns. Although some of them have a diet richer in carbohydrates obtained from agriculture, (Ssj) others have a diet richer in proteins obtained from hunting (Nv).

Along the CW, an important intraregional variation can be seen. This region constitutes the southern boundary of Pre-Hispanic maize agriculture, along the Andes of San Juan and Mendoza. Archaeological evidence from San Juan (Nsj, Ssj) supports the notion that those populations could have combined agriculture with a pastoralist strategy (Castro et al., 2013; Gasco, 2014). Despite the intake of proteins from pastoralism, the reliance on carbohydrates among agriculturalists has been regarded as the main reason for high rates of dental caries, similar to what other studies around the world have posited (Cohen and Armelagos, 1984; Hillson, 1979; Larsen et al., 1991; Meiklejohn et al., 1984; Milner, 1984; Newbrun, 1982; Turner, 1979; Ubelaker, 1978). This accounts for the high rates of dental caries of some samples (Ssj), although some have lower rates than expected (Nsj). These trends are confirmed by the $\delta^{13}C$ values, which average -13.3 for Nsj samples (Gil et al., 2014). Archaeological evidence regarding the populations of Mendoza (Nmz, Smz) allow us to interpret a mixed subsistence strategy, which includes hunter-gathering, fishing, and the incorporation of maize to the diet (Gil, 2003; Gil et al., 2006, 2011; Neme and Gil, 2008). However, in spite of the isotopic and archaeobotanic evidence of maize consumption, there is no evidence of cultivation *in situ*. Thus, archaeologists interpreted the role of maize in the diet of the prehistoric populations of Mendoza as negligible (Novellino et al., 2004), although people from North Mendoza (Nmz) could have had diets richer in carbohydrates than those from South Mendoza (Durán, 2000; Gil et al., 2011). Given the lack of evidence of cultivated areas and irrigation technologies, three hypotheses were suggested for the presence of cultigens in Mendoza: (a) they were obtained through trade with Northern groups (Gil et al., 2010; Maferra, 2009); (b) they were cultivated in small-scale spaces with natural water (Prieto, 1985); or (c) the $\delta^{13}C$ data that had a strong C4 plants signal could be interpreted as the result of a diet based on camelids' proteins which, in turn, had a diet based on C4 plants (Gil et al., 2016). However, there is insufficient evidence to fully support any of these explanations.

Conversely, research from Pampa and northern Patagonia (PA, NP) supports the idea that those populations had a mixed diet as a result of the high consumption of wild plant resources with carbohydrate content, obtained either locally or as a result of trade with other groups (Bernal et al., 2007; Menéndez, 2010; Menéndez et al., 2009; Musaubach and Berón, 2011; among others). Additionally, the ethnohistorical record mentioned that Patagonian Araucanian groups may have cultivated local species such as mango (*Bromus mango*), teca (*Bromus berteroanus*), lanco (*Bromus catharticus*), and madi (*Madia sativa*) (e.g., Bibar, 1966 [1558]; Valdivia, 1929 [1550–1554]). So, samples that had high rates of dental caries (A, Lm) could be explained by the consumption of these wild plants. This is consistent with the results of Humphrey et al. (2014), which found high prevalence of dental caries among Pleistocene hunter-gatherer populations of North Africa. This may be interpreted as a product of the consumption of wild plants rich in fermentable carbohydrates. Nevertheless, some of PA and NP samples present extremely low rates of dental caries (Lj, Nv), as it is expected for hunter-gatherer populations (Turner, 1979). The variation in dental caries of hunter-gatherers is described in the work of Sealy et al. (1992), who investigated rates of dental caries in the hunter-gatherer populations of the coast of Cape Province, in South Africa. The results show that, while hunter-gatherers who fed on fish have the lowest rates of dental caries, hunter-gatherers with a more terrestrial diet have the highest rates of dental caries, which is interpreted as a product of variations of the fluoride content of the water they drank. This means that in small areas, rates of dental caries of hunter-gatherers could experience wide variations, which stands in opposition to prevailing ideas which associate low rates of dental caries to hunter-gatherer groups. As Tayles et al. (2000) have previously stated, however, it should not be assumed that all crops are correlated with high dental caries rates, as studies of populations with rice-based diets demonstrate. Following these ideas, while high rates of PA samples (A) could be explained by the consumption of wild cariogenic plants, low rates in some NP samples (Sb, Nv) could be explained by a reliance on a fish diet or the consumption of plants and/or crops with a low cariogenic effect.

The distribution of dental caries rates obtained here suggest more variability in how we understand and define subsistence strategies. Together with other works (Humphrey et al., 2014; Tayles et al., 2000, 2009), the results presented here challenge the common assumption that high rates of caries are always indicative of agriculture groups and low rates of caries are related to hunter-gatherer populations, as has been argued before. According to this dichotomy, intermediate dental caries values would be expected in mixed subsistence groups, a premise that this work demonstrates is not always the case. Also, these results are not consistent with Turner's classic paper about subsistence strategies (1979). When comparing samples that had different subsistence strategies, he established a set of expected ranges of dental caries rates (based on the number of carious teeth in relation to the number of teeth that were present) according to their diet, averaging 1.72% for hunter-gatherer populations, 4.37% for mixed foraging-farming, and 8.56% for fully agricultural populations. Results here show that the latter is not always the pattern. Hunter-gatherers were shown to have 9.45% of dental caries (Sc1), populations with mixed subsistence 11.76% of dental caries (Lm), and agriculturalists 3.28% of rates of dental caries (Nsj). The accepted wisdom that the introduction of agriculture promoted higher frequencies of carious lesions seems to have its roots in New World agricultural centers that existed at the time of Spanish contact (Mesoamerica and Central Andes), where the dietary shift toward maize had a significant impact on the prevalence of caries of those populations (Eshed et al., 2006). However, it appears that it was not a worldwide phenomenon. In the Old World, Neolithic domesticated resources (e.g., cereals and fruits) were either less cariogenic or had less dietary importance than maize in North America (Lubell et al., 1994) and, in Southeast Asia, rice farming did not appear to involve the increase of dental caries (Tayles et al., 2000, 2009).

In prehistoric Argentinian populations, frequencies of caries should be interpreted as influenced by a complex set of factors, particularly when considering groups with mixed subsistence. Low rates of caries do not warrant excluding cultigens as a contributor to the diet of hunter-gatherer or mixed-subsistence populations, and the presence of high rates of dental caries should not be interpreted as a diet based on domestic plants. Additionally, other studies have shown that the frequencies of eating, methods of food preparation, and the retention of food in the mouth are additional factors which contribute to an overall prevalence of caries (Lingstrom et al., 2000), which demonstrates that cultural practices play an important role on dental caries expression. Beyond that, dental caries is a multifactorial disease that results from the interaction of numerous intrinsic factors, such as salivary flow rate, pH, and tooth morphology, as well as environmental factors—such as exposure to different levels of fluoride in water (Lukacs et al., 1985; Molnar and Molnar, 1985; Tayles et al., 2009), and the presence of abrasive particles in the diet. Several studies on various prehistoric populations (Lukacs et al., 1985; Molnar and Molnar, 1985) demonstrated that high levels of fluoride prevent caries, while low levels of fluoride foster it. In addition, diets that are high in hard abrasives, due to the stone tools used during preparation and cooking techniques, can reduce caries formation because the mastication of grit particles wears down enamel surfaces, thereby preventing or abrading carious lesions (Hillson, 2001, 2008). Another aspect to be considered relates to carbohydrates themselves: while sugar is highly cariogenic, starch is relatively mildly cariogenic, but starch, consumed together with sugar, increases cariogenicity (Moynihan et al., 2004). Further chemical studies are needed to investigate the cariogenic potential of the diet consumed by prehistoric Argentinian populations, particularly local plant species with a carbohydrate or a starch component. These studies, together with the contextual analysis of other archaeological remains, will help to explain the dental caries rates present in late Holocene populations of southern South America.

CONCLUSION

This study provides evidence for a relatively strong geographical pattern of dental caries variation in late Holocene prehistoric populations of southern South America. While northern and southern populations represent the highest and lowest extremes of the dental caries rates, samples from the central region disrupt this continuity. In that area, some samples present both high and low dental caries rates. The coexistence of those values could be explained by the subsistence strategies of the different human groups analyzed. In these samples, while high dental caries rates were explained by the consumption of wild cariogenic plants or cultigens obtained either locally or through trade, low rates could be explained by a reliance on fishing or the incorporation of plants rich in starch rather than simple carbohydrates. It is recommended that dental caries be treated as a multifactorial disease which results from the interaction of both cultural practices and environmental factors, and that dental caries should be analyzed using approaches that examine subsistence strategies. Due to the importance of cultural practices, as well as available resources and subsistence strategies of the studied populations, the present study supports others in the assessment that prehistoric diets should be interpreted along with other variables, including contextual archaeobotanical and zooarchaeological evidence, as well as isotopes and other bioarchaeological variables.

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