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Peopling time, spatial occupation and demography of Late Pleistocene–Holocene human population from Patagonia



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ABSTRACT

The settlement of Patagonia has been the subject of extensive research, although key questions about the timing of arrival of the first humans and the subsequent patterns of dispersal and demographic changes within the region remain largely unresolved. In this study we evaluated the most probable date for the initial peopling of Patagonia and explored the temporal and spatial changes in population size along Late Pleistocene–Holocene by using robust statistical methods for the analysis of radiocarbon dates and molecular data. We suggest that the first humans probably arrived to Patagonia around 17,000–14,000 years BP, a few thousands of years earlier than generally stated. Within the region, the populations experienced a sustained and slow growth until the transition Pleistocene–Holocene, when the population size started to increase, with a remarkable acceleration after 7000–5000 years BP and reaching its maximum at 1000 years BP. The spatial occupation was not homogeneous across the region though, changing from a more intense continental occupation to a coastal occupation in the Late Holocene. This pattern of peopling and population expansion, obtained here on the basis of a rigorous and comprehensive quantitative approach, will allow the future evaluation of formal models about the ecological and cultural processes that drove the evolution of the human populations from Patagonia.

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1. Introduction

Patagonia was the last continental region of the world to be colonized by modern humans. The archaeological evidence most widely accepted suggests that they spread into the region from the Northwest of South America by around 14,000 years ago, probably following the Pacific coast and reaching southern Patagonia ca. 13,000 years ago (Miotti and Salemme, 2003; Steele and Politis, 2009; Prates et al., 2013). There is increasing genetic data, from modern and ancient mtDNA and Y chromosome, supporting that

the early populations that inhabited the region descended from Asian groups. This evidence also points out that early populations probably gave rise to Late Holocene and historic populations, suggesting a local biological evolution of Patagonian groups (Moraga et al., 2000; Garcia-Bour et al., 2004; Goebel et al., 2008; Perego et al., 2010; Bodner et al., 2012; de Saint Pierre et al., 2012a). The spatial pattern of early human occupations in Patagonia seemed to have occurred almost simultaneously along the Atlantic and Pacific coasts, while the Andean foothills were colonized much later (Borrero, 1994–1995; Miotti and Salemme, 2003; Prates et al., 2013). Previous studies also postulate that human populations were small and stable along Late Pleistocene and Early Holocene, and that an increase in the occupation density only occurred during the Late Holocene, particularly during the last 1000 to 500 years BP (Martínez et al., 2013; Barberena et al., 2015; Zubimendi et al., 2015). It has also been postulated that in some areas of Patagonia population density decreased during the Middle Holocene

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(Barrientos and Perez, 2005; Neme and Gil, 2008; Salemme and Miotti, 2008). In spite of these apparent agreements, the timing and process of peopling as well as demographic changes in Patagonia have been the focus of intense debate for the last decades (Kelly, 2003; Goebel et al., 2008; Salemme and Miotti, 2008; Dillehay, 2009; Steele and Politis, 2009; Méndez et al., 2015).

In order to address these issues, significant effort has been devoted to obtain extensive databases of radiocarbon dates, while the conceptual and methodological approaches to analyze them have received less attention. In this sense, the pattern of dates is usually taken as a direct evidence of the initial peopling and demographic dynamic of the Patagonian populations. However, these assumptions are at least arguable. First, it has long been accepted that the archaeological record is incomplete and longtime gaps may exist between the oldest known archaeological evidence and the initial peopling (Marshall, 1990; Saltré et al., 2015; Villavicencio et al., 2015). Therefore, the earliest dated site cannot be assumed as the evidence of the first peopling in a given region. Additionally, it is widely recognized that the taphonomic processes, sample size and sampling strategies of radiocarbon dates can generate biases in the estimations of the spatial occupation and demographic dynamics of hunter-gatherer groups (Williams, 2012; Timpson et al., 2015; Torfing, 2015). Given that these conceptual and methodological problems have not been taken into account in previous studies, the temporal and spatial processes of Patagonian peopling are far from being well described and understood.

In this study, we estimate the most probable time for the earliest peopling of Patagonia and explore the temporal changes in population size along Late Pleistocene–Holocene by using robust statistical methods for the analysis of radiocarbon dates. We also investigate the temporal changes in the spatial occupation and population density of the region. In addition, we obtained independent estimations of the earliest peopling and posterior demographic changes using molecular data. Here we study the peopling time, spatial occupation (or geographic distribution) and demography together because they are part of the same process of colonization and posterior population dynamic in a region (Drummond et al., 2005; Avise, 2009; Lemey et al., 2009). To investigate the time and temporal dynamic of peopling we assembled a comprehensive dataset of radiocarbon dates of archaeological sites from the southern cone of South America and analyzed them by means of time series and stratigraphic statistics (Marshall, 1990; Surovell and Brantingham, 2007; Williams, 2012; Shennan et al., 2013; Saltré et al., 2015). The spatial occupation of the region was explored using the distribution of the frequency of radiocarbon dates employing spatial statistical analyses (Legendre and Legendre, 1998). The molecular-based estimations of the earliest time of Patagonian peopling and the posterior demographic changes were performed using modern and ancient mtDNA data and Bayesian methods (Drummond et al., 2005; Ho and Shapiro, 2011; Perez et al., 2016).

2. Material and methods

2.1. Radiocarbon and molecular data

We assembled a dataset of 1785 radiocarbon dates from different bioarchaeological and archaeological sites from South Buenos Aires and Mendoza to Tierra del Fuego (between 36 and 55 degree of South Latitude; Fig. 1; Table A.1; Borrero and Franco, 2000; Gil, 2006; Salemme and Miotti, 2008; Tessone and Belardi, 2010; Boschín and Andrade, 2011; Morello et al., 2012; Fernández et al., 2013; Martínez et al., 2013; Prates et al., 2013; San Román, 2013; Gil et al., 2014; Pallo and Ozan, 2014; Barberena et al., 2015; Berón, 2015; Campbell and Quiroz, 2015; García Guraieb et al., 2015; Martínez et al., 2015; Zubimendi et al., 2015; Perez

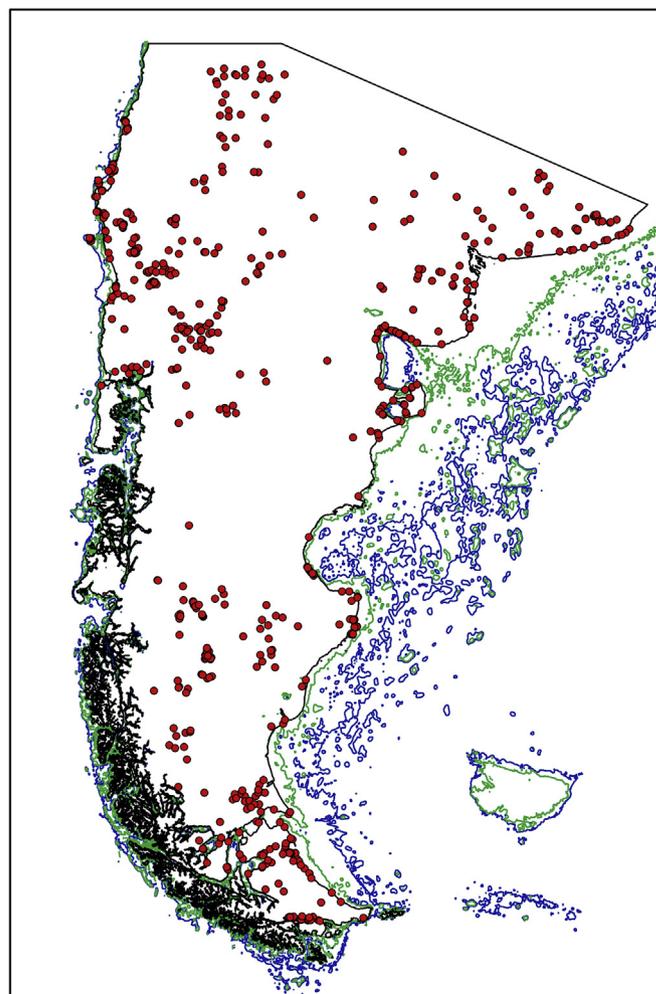


Fig. 1. Distribution of studied archaeological sites (red points), current coastline (black line) and the estimated coastlines at 11,500 Cal BP (green line) and 17,000 Cal BP (blue line). The coastlines are drawn following Prates and collaborators (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2016). Sites from neighbor areas such as Southern Cuyo and South Pampa were also included because they have been previously discussed together with Patagonian sites in studies that address the peopling of this region. The final dataset was generated after eliminating dates of the same site that overlapped in the informed standard deviation, including in the dataset the dates with the narrower standard deviation. In this way, we avoid possible biases related to the intensity of excavation in the same archaeological site or the quantity of economic resources invested for investigating specific periods of greatest interest (e.g. the early peopling of the region). All dates were calibrated using the Calib 7.0 software and the *SHCal13* Southern Hemisphere Calibration Curve (Stuiver et al., 2014).

Modern and ancient human mitochondrial DNA (mtDNA) sequences were downloaded of the GenBank database and of previous publications (Table A.2; Ginther et al., 1993; Moraga et al., 2000; García-Bour et al., 2004; Perego et al., 2009; Bobillo et al., 2010; Moraga et al., 2010; Catelli et al., 2011; Bodner et al., 2012; de Saint Pierre et al., 2012a, 2012b; de la Fuente et al., 2015). We analyzed sequences from descendants of aboriginal populations carrying mtDNA variants (haplotypes) with high frequencies and/or mainly restricted to populations from the extreme south of South

America. The 295 studied sequences comprise 1016 base pair (bp) corresponding to the mtDNA control region (rCRS positions approximately between 16,024 and 576) and were aligned with MAFFT v7.012b, using the default setting (Katoh and Standley, 2013). Sequences from cosmopolitan populations and haplotypes with high frequency outside Patagonia were not included in the analyses.

2.2. Radiocarbon based analyses

2.2.1. Time of the earliest peopling

If the initial peopling of Patagonia was by very small and highly mobile groups of hunter-gatherers, it is likely that their archaeological record would be sparse and the chances of being discovered very low (Borrero, 1989–1990, 2009). With an incomplete archaeological record, the oldest radiocarbon date in a region is typically posterior to the actual time of the first arrival of human groups into the region. In that case, the estimation of the timing of initial peopling should incorporate the uncertainties imposed by the characteristics of the formation process of the archaeological record. This can be achieved by adding confidence intervals to the end of the range of strata with evidence of occupation. Here, we applied the frequentist method of Confidence Intervals on Stratigraphic Range implemented in PAST 3.09 (Hammer et al., 2001; Hammer and Harper, 2006), based in the methods proposed by Strauss and Sadler (1989) and Marshall (1990). To estimate the confidence intervals for the temporal depth of the archaeological record in a given area this method takes into account the dates of the first and last occupied strata, and the total number of strata with evidence of occupation. The method assumes that the deposition of archaeological remains follows a random (Poisson) distribution, where the earliest events have a lower probability of deposition (Hammer and Harper, 2006). The earliest evidence of occupation was established alternatively in 13,000 and 14,000 years, using the most robust and conservative evidence of radiocarbon dates for the southern cone of South America (Steele and Politis, 2009). The estimation of the stratigraphic sequence of Patagonia was based on caves with well-established sequences and reliable radiocarbon dates (e.g. Piedra Museo, Fell, CCP7 caves; Emperaire et al., 1963; Miotti, 1996; de Nigris, 2004; Marchionni, 2013). These sites have between 10 and 20 strata; therefore, the estimations were made using a range of strata values to assess the effect of the number of strata used on the estimations of the confidence intervals.

The methods of Strauss and Sadler (1989) and Marshall (1990) have been criticized because they do not incorporate the uncertainties associated with the radiometric dates and assume that the likelihood of finding evidence of occupation is the same along the true range. However, it is well known that this probability increases as the region is occupied and varies in relation to changing taphonomic conditions (Villavicencio et al., 2015). To formally incorporate these factors in our estimations, we also infer the time of the initial peopling of Patagonia employing one method implemented by Saltré and collaborators (2015) provides a 95% confidence band around the estimated time of peopling. This method, called Gaussian-resampled inverse-weighted method (GRIWM), deals with non-random deposition of archaeological remains by progressively up-weighting the gap sizes the closer they are to the time of the initial peopling (Bradshaw et al., 2012). This estimation was then compared to the results obtained with the methods of Strauss and Sadler (1989) and Marshall (1997) implemented by Saltré et al. (2015). These estimations were obtained in the R software (R Development Core Team., 2015). We used as input the twenty two earliest dates (>13,000 Cal BP) for the archaeological sites Arroyo Seco 2, Pilauco, Cerro Tres Tetras, Cueva Lago Sofia 1, Monte Verde Component II, Tres Arroyos, Cueva del Medio,

Chinchihuapi, Los Toldos, and Piedra Museo AEP-1 (Table A.1). Alternatively, we employed fifteen less controversial radiocarbon dates between 11,900 and 11,000 C14 BP (13,700 and 12,900 Cal BP; Steele and Politis, 2009) from the following sites: Tres Arroyos, Cueva del Medio, Pilauco, Cerro La China-Sitio 2, Cerro Tres Tetras, Arroyo Seco 2, Cueva Lago Sofia 1, Monte Verde Component II.

2.2.2. Spatial distribution of radiocarbon dates

The spatial distribution and density of calibrated dates along time was explored using geographic distribution maps. The sites were geo-referenced using the Gauss Krueger projection (Argentina), Sash 3 Datum: WGS84. We divided the dataset in periods of 2000 years and superimposed a grid of 100×100 km of size on the maps of distribution of radiocarbon dates (Fig. 1 and Fig. A.1). To select the size of the cells we considered that they were not too large, resulting in excessive loss of localized information, or too small to generate artificial spatial discontinuities in the distribution of sites. The frequency of sites by period was recorded for each cell and then plotted against the mean geographical position of the cells. To obtain a continuous distribution of frequency values across the entire region, we estimated the frequency of dates for each pixel on a map of Patagonia by interpolating the observations available in neighbor areas of the mean position of each cell using the inverse distance-weighting approach (Legendre, 1993; Legendre and Legendre, 1998). We set the 'search circle' around each pixel using a maximum of 12 neighbor cells and a minimum of nine neighbor cells to be included in each interpolation value. For each pixel, an estimated value (\hat{y}) was assigned by using the weighted mean of the neighbor observations within the search circle; $\hat{y} = \sum w_i y_i$, where y_i is an observed value in the circle and w_i is the inverse of the distance between the observed value and the frequency to be estimated. This interpolation plot method generates a more robust and smooth estimation of site distribution and has been widely applied in ecology (Legendre, 1993). The method assumes that the estimated frequency for the pixels is likely to resemble the frequencies of the cells of the same local area, and that the differences in the frequency of sites among cells are in an inverse proportion to the distance between them.

For each period, we also estimated the distribution of distances from each site to the sea coast—past and present coastline—as Euclidean distances considering a variable search radius. All the analyses were performed in the Quantum GIS v2.8.5 software (QGIS Development Team, 2015).

2.2.3. Temporal distribution of radiocarbon dates

To explore the pattern of temporal changes in the occupation of Patagonia we employed time distribution graphs (Surovell and Brantingham, 2007; Williams, 2012; Shennan et al., 2013). Specifically, the calibrated dates were graphed using histograms to generate curves of densities of occupation throughout time, which indirectly allowed us to explore temporal changes in human demography. The radiocarbon dates were 'data binned' into 400 year intervals to reduce the effect of sampling bias. We considered the impact of type of archeological site, a taphonomic factor that might have an effect on the density curves of radiocarbon dates, by estimating the temporal distribution of open air, rockshelter and cave sites. We also corrected the number of dates at each time interval t by dividing the observed number of dates in each interval by the empirically derived expectations suggested by Surovell et al. (2009; S2009), where the expected $nt = 5.726442 \times 10^6 (t + 2176.4)^{-1.3925309}$. The distribution of temporal frequencies of radiocarbon dates was smoothed by the common and simple n -point centered moving average, with a n value of five (Hammer and Harper, 2006).

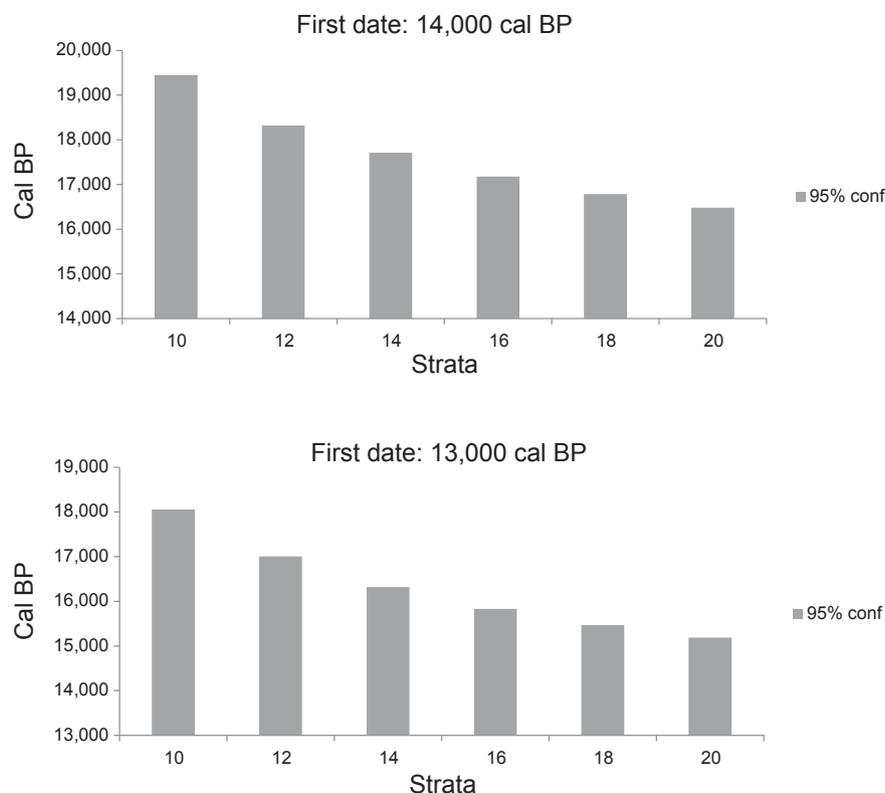


Fig. 2. Estimated age for the first peopling of Patagonia based on Confidence Intervals on Stratigraphic Range method. The upper panel shows the estimations based on an ancient age of 14,000 Cal BP, while the lower panel displays the results obtained for the most accepted date of 13,000 Cal BP (Steele and Politis, 2009). The most probable age was estimated considering a range of strata values between 10 and 20.

Finally, to test if the trend observed in the distribution of radiocarbon dates was positive and significant we applied the non-parametric Mann–Kendall test (Gilbert, 1987). The S statistic was calculated by summing over all pairs of values, $S = \sum_{i=1}^{n-1} \sum_{j=i+1}^n \text{sgn}(x_j - x_i)$. The sign of the S value is informative of the sign of the trend. The significance of S was established using the Z statistic. The statistical analyses were performed in PAST v. 3.09 (Hammer et al., 2001) and R software 3.0.3 (R Development Core Team., 2015).

2.3. Molecular-based analyses

2.3.1. Time of coalescence and demographic inference

The molecular sequences were used to estimate the time of coalescence of haplotype mtDNA lineages and demographic trajectories of human populations from Patagonia employing Bayesian methods (Drummond et al., 2005, 2006). We estimated genealogical trees with time of divergence by haplotypes using the method developed by Drummond et al. (2006). We employed a relaxed molecular clock model, which allows substitution rates to vary across lineages according to an uncorrelated lognormal distribution (Drummond et al., 2006), and set the tree priors as a Yule Process. The Bayesian Skyline Plot method (BSP; Drummond et al., 2005) was used to estimate changes in population size along Late Pleistocene and Holocene. This method uses the coalescent theory to relate the shape of a molecular genealogy to the demographic dynamic of the populations in the past (Drummond et al., 2005; Ho and Shapiro, 2011).

We generated the genealogical tree and the Skyline Plot using the Bayesian approach implemented in BEAST 1.6.1 (Drummond and Rambaut, 2007), which uses a Markov chain Monte Carlo

(MCMC) sampling procedure to estimate the genealogy, coalescence time and the population size—as well as its credibility intervals—through time from the molecular sequences (Drummond et al., 2005, 2006). The MCMC simulations were set in 50,000,000 generations and a sample frequency of 5000 (Rambaut and Drummond, 2007). The BSP analyses and genealogical estimations were performed assuming a HKY model of mtDNA sequence evolution and rates of substitutions by site by year of $2.4\text{E-}7$ and $3.02\text{E-}7$ (s/s/y; Santos et al., 2005; Endicott and Ho, 2008; de Saint Pierre et al., 2012a, 2012b; Perez et al., 2016). We employed Tracer v1.5 (Rambaut and Drummond, 2007) to evaluate convergence in the MCMC simulations and to generate the BSP plot. The genealogies were explored with the software FigTree v1.4.

3. Results

3.1. Time of the earliest peopling

Based on radiocarbon dates and Confidence Intervals on Stratigraphic Range analyses, we suggest that the most probable time (i.e. the 95% confidence interval) for the earliest peopling of Patagonia was between 16,000 and 13,000 years ago or between 18,000 and 14,000 years ago, considering a minimum age of either 13,000 or 14,000 Cal BP, respectively, and 14 or 16 strata (Fig. 2). The most ancient value increase or decrease according to the amount of archaeological strata considered in the analysis (Fig. 2). The results obtained with the Saltré et al. (2015) approach also suggest an initial peopling between 18,000 and 14,000 Cal BP (Table 1). This time exceeds the previous evidence based on the first occurrence of archaeologically well-supported dates, around 14,000 and 13,000 years ago (Steele and Politis, 2009; Prates et al., 2013).

Table 1
Estimated interval for the earlier Patagonian peopling based on the approaches of Strauss and Sadler (1989), Marshall (1997) and GRIWM (Bradshaw et al., 2012), using the most conservative and the more controversial radiocarbon dates (Steele and Politis, 2009).

Method	Dates >13,000 Cal BP		Dates >11,000 and <12,000 C14 BP	
	Calibrated younger age	Calibrated oldest age	Calibrated younger age	Calibrated oldest age
<i>Strauss-Sadler</i>	16,289	16,795	13,658	13,880
<i>Marshall</i>	16,283	18,433	13,657	14,471
<i>Griwm</i>	17,031	17,044	14,036	14,042

Interestingly, our earlier estimation based on radiocarbon dates is within the range of results obtained with molecular data (Table 2). In Table 2 we show the Time of the Most Recent Common Ancestor of the lineages B2l, C1b13, D1g and D4h3a5, that previous studies suggest were originated within Patagonia (Bodner et al., 2012; de Saint Pierre et al., 2012a). Because there is no agreement about the most adequate substitution rate, we compared the ages obtained with two different rates [2.4E-7 (Santos et al., 2005) and 3.02E-7 (Endicott and Ho, 2008) s/s/y]. Taking the substitution rate from Santos et al. (2005) we obtained the most ancient ages of 17,266 and 15,632 years for C1b13 and D1g, respectively. The haplotypes B2l and D4h3a5 display younger ages, of 13,674 and 10,852 years, respectively. The estimations using the Endicott and Ho (2008) rates were in average 3000 younger (Table 2). Therefore, these results suggest that the region was peopled between 17,000 and 14,500 years ago, considering the probable time interval of the earliest lineage divergence within the region (the C1b13 haplotype).

Table 2
Coalescence ages of the mtDNA variants (haplotypes) with high frequencies and/or mainly restricted to populations from the extreme south of South America. The ages were calculated using two different mutation rates, Endicott and Ho (2008; 1) and Santos et al. (2005; 2).

Haplotypes	Mutational rates	
	0.302 s/s/y ²	0.24 s/s/y ³
B2l	10,872	13,674
C1b13	14,522	17,266
D1g	12,120	15,632
D4h3a5	7848	10,852

3.2. Pattern of spatial occupation

Fig. 3 displays the temporal changes in the density of radiocarbon dates, as indirect evidence of human occupation, using artificial intervals of 2000 years. The patterns of spatial occupation along time do not show simple latitudinal or longitudinal trends. During the period 16,000–14,000 years, the sites were concentrated in the Pacific coast, considering the unique evidence of sites in the Monte Verde locality. In the next period, 14,000–12,000 years ago, additionally to the Pacific occupation, the Atlantic coast displays evidence of occupation, particularly in Southeast Pampa, Northeast of Santa Cruz and in both sides of the Magellan strait (Fig. 3). During the next periods (between 12,000 and 8000 years) the interior of the continent began to be peopled, being the first evidence found in Northwest Patagonia and the Central Plain in Santa Cruz. Between 8000 and 4000 years ago, the human population started to occupy the southernmost part of Andean mountains and the density of occupation in Tierra del Fuego increased. In the last 4000 years all the Atlantic coast was occupied and the density of sites increased significantly across Patagonia. Only the Central Plain of Chubut, the Central Pampa and the Somuncurá Plain in Río Negro show low density of sites during all periods.

The distribution of distances to the sea shows that during the early peopling almost all sites were closer than 150 km to either the Atlantic or Pacific sea (Atlantic and Pacific; Fig. A.2). During the Late Pleistocene and Early Holocene (12,000–8000 years BP) the sites were homogeneously distributed between 0 and 350 km from the sea. After 8000 years BP and during the Middle and Late Holocene the sites were concentrated in the coast, between 20 or 30 km to the sea (Fig. A.2).

3.3. Demographic changes

The Mann–Kendall test shows that the positive trend observed in the distribution of radiocarbon dates for all types of sites is significant (Cave: $S = -505$, $P < 0.0001$; Rockshelter: $S = -582$, $P < 0.0001$; Open air: $S = -648$, $P < 0.0001$). Fig. 4 displays the demographic reconstruction based on calibrated radiocarbon dates for the different types of sites using data uncorrected and the S2009 correction for taphonomic bias. The curve estimated using cave dates displays an increase in population size between 14,000 and 12,500 years ago, then no changes in population size are observed until 4000 years ago, when a steady increase occurs (Fig. 4). Uncorrected rockshelter and open air sites only display an increase in population size around 4000 years ago. However, the use of the correction method proposed by Surovell et al. (2009; S2009) results in a curve more similar to that obtained with the cave data (Fig. 4). Interestingly, this correction generates more sudden fluctuations in the frequency of sites than the uncorrected data, as can be seen, for instance, around 10,200 and 3500 years BP. Such fluctuations are probably related to sampling bias of radiocarbon dates (Perez et al., 2016).

The Bayesian Skyline plot (BSP) based on molecular data shows that the human population from Patagonia had a female effective population size of ca. 1200 individuals during the Late Pleistocene, 16,000 years ago, and it increased slowly between 12,500 and 6000 years ago, being this change more noticeable after 7000–5000 years ago (Fig. 5). The population reached an estimated female effective population size of 10,500 individuals ca. 2500 years ago. Then, it continued growing until reaching a size of 20,000 individuals ca. 500 years ago. The confidence intervals generated by the BSP progressively increase from 350 to 7000 individuals by 16,000 years BP to 7000–70,000 individuals by 500 years ago (Fig. 5).

4. Discussion

In this work we present an analysis of an extensive dataset of published radiocarbon dates from recently excavated archaeological sites and mtDNA sequences of modern and ancient aboriginal populations from Patagonia, southern South America. To the best of our knowledge, this is the first study that comprehensively explores the time of peopling, the spatial occupation and changes in human demography in Patagonia. These problems have been mainly addressed using radiocarbon dates only at regional scales (Martínez et al., 2013), or datasets restricted to Late Pleistocene and Early

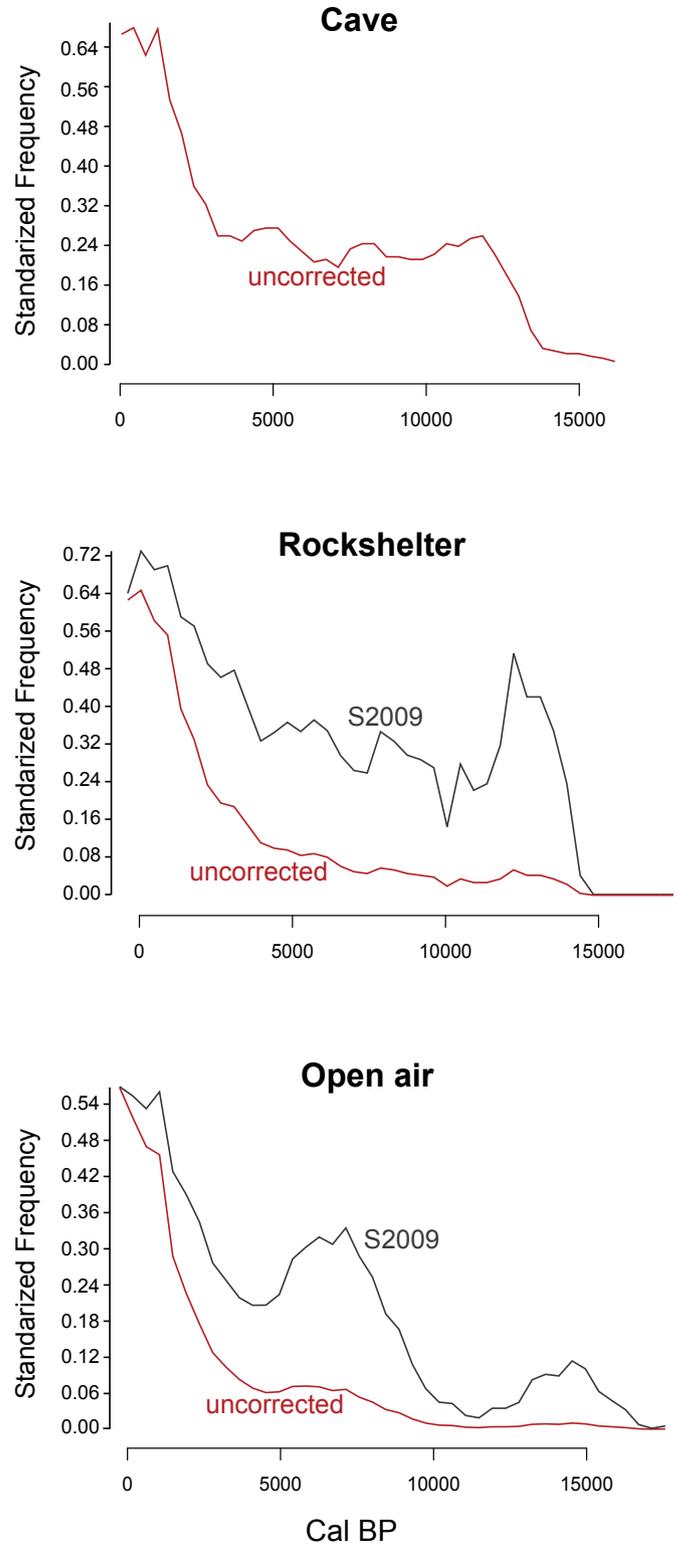
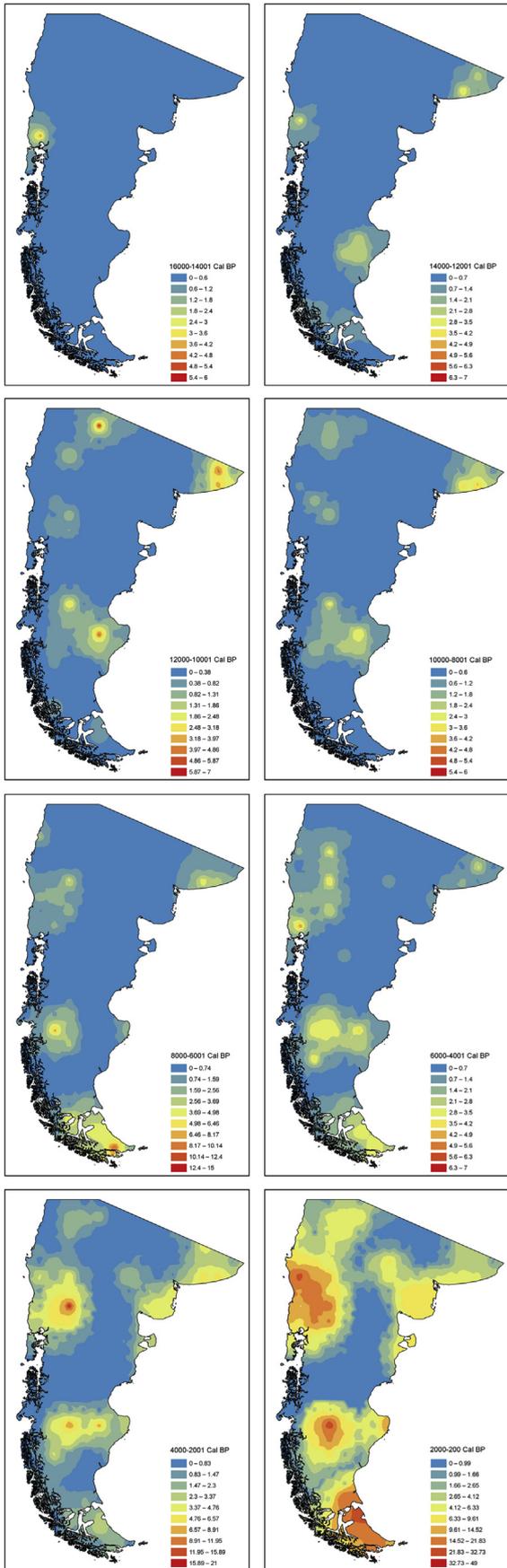


Fig. 4. Demographic reconstructions based on calibrated radiocarbon dates of caves, rockshelters and open air sites. For the last two types of sites, the estimations using corrected data for taphonomic bias with the method of Surovell et al. (2009; S2009) are also shown.

Fig. 3. Spatial patterns of the frequency of sites in Patagonia. The map of the density of sites was created for eight temporal intervals using interpolating methods with the inverse distance-weighting approach.

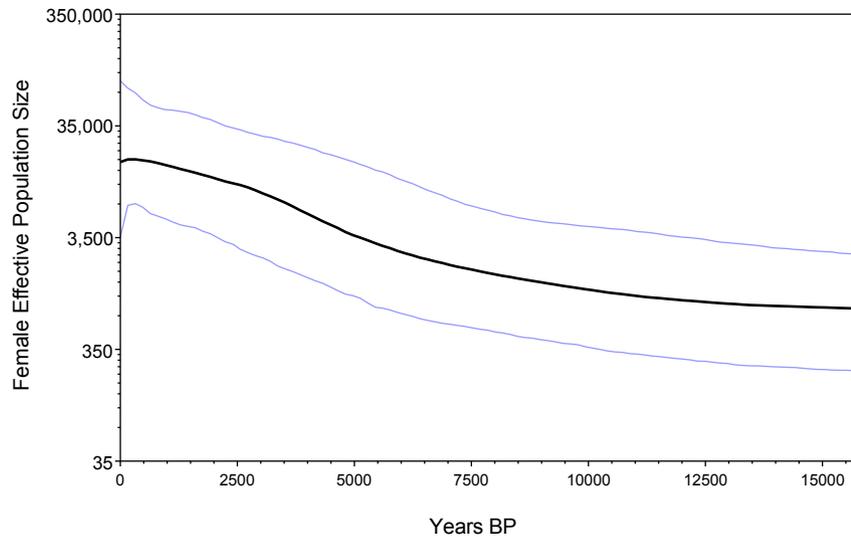


Fig. 5. BSP reconstruction of the human demographic curve based on modern and ancient mtDNA control region. The analysis was performed using the sequences from descendants of aboriginal populations of Patagonia having mtDNA variants (haplotypes) with high frequencies and/or mainly restricted to the extreme south of South America.

Holocene periods (Miotti and Salemme, 2003; Steele and Politis, 2009; Prates et al., 2013).

The confidence intervals obtained for the earliest and strongly supported radiocarbon dates, as well as the estimation of the time of the most recent common ancestor of the mtDNA lineages specific of Patagonia, suggest that the initial peopling of the region occurred between 17,000 and 14,000 years ago. Previous analyses of mitochondrial lineages exclusively distributed in southern South America (Bodner et al., 2012; de Saint Pierre et al., 2012a) agree with our results. Particularly, these studies show that some haplotypes such as B2I, C1b13 and D1g—which present large variation, have high frequencies in current populations, are observed in ancient DNA and are mainly restricted to populations from the extreme south of South America—have a range of ages between 19,000 and 14,000 years ago, when the substitution rates employed in our work are used, or are even much older when considering the substitution rate suggested by Soares et al. (2009). We estimate similar ages employing a more comprehensive dataset of sequences, showing that these estimations are very robust. Interestingly, this estimation agrees with the controversial dates of the archaeological site Monte Verde (Chile), whose Component II has calibrated dates between 18,500 and 14,500 Cal BP (Dillehay et al., 2015), as well as with Piedra Museo and Pilauco with dates around 15,000 Cal BP (Miotti et al., 1999; Pino et al., 2013). However, our results cannot be interpreted as evidence supporting the veracity of the earliest radiocarbon dates from those archaeological sites.

Our estimations of the earliest peopling event are outside of the values presented by most archaeological studies. Particularly, Steele and Politis (2009) suggest, based on samples with strong anthropic evidence (hearth charcoal and cut-marked bone), that human populations were in the southern cone of South America at or soon after 13,000 Cal BP. They suggest that this is the time of funding of “a persistent and demographically viable hunter-gatherer population” (Steele and Politis, 2009). However, the evidence analyzed here suggest that the human population of Patagonia was experiencing a demographic growth by that time, remaining then relatively stable until the end of the Middle Holocene (Figs. 4 and 5). Therefore, the apparent discrepancies between the ages suggested by recent archaeological studies and the estimations obtained here can be solved if we consider that the interval between our earliest

dates and the first population growth—the time of peopling supported by Steele and Politis (2009)—was probably the time of the initial spreading of humans in a previously empty area (Borrero, 1994–1995), where the chances of finding archaeological remains are very low.

After 13,000 Cal BP, radiocarbon dates and molecular data suggest that Patagonia was stably occupied by a human population that grew slowly. Radiocarbon dates for cave sites show this pattern more clearly. The radiocarbon distributions of the rockshelter and open air sites after taphonomic correction suggest a similar pattern. However, some peaks and valleys observed in the open air and rockshelter distributions of radiocarbon dates should be interpreted with caution, specifically the peak around 12,500 Cal BP in the rockshelter distribution and the peak around 7500 Cal BP in the open air data (Fig. 4), because they can be the result of over-correction of the S2009 formulae (Williams, 2013). Even considering the limitations of the different datasets and corrections, the results for the population changes along Late Pleistocene and Early Holocene are generally concordant. Our results also show that although the population grew constantly along the Holocene, the largest population increase began after 7000–5000 Cal BP, reaching the maximum size at 1000 Cal BP (Figs. 4 and 5). For the Late Holocene we estimated a population density between 5 and 20 individuals/100 km², which represents a 30 fold increase compared to the density calculated for the Late Pleistocene. Importantly, this trend can be observed in molecular, and also in the S2009 corrected and uncorrected radiocarbon data, indicating that the pattern of population growth during the Late Holocene is not a result of taphonomic effects or other biases. The rapid increase in the population of Patagonia can be seen more clearly in radiocarbon data.

Along with the demographic changes that took place during the Late Holocene, there was an increasing use of landscapes previously empty, suggesting that this was a period of intensification in the human occupation and use of resources, i.e., the effective occupation phase described in previous studies (Borrero, 1989–1990, 1994–1995). During this time of rapid population growth, the human settlements were increasingly concentrated in the coast of the sea, between zero and 30 km (Fig. 3 and Fig. A.2). This spatial pattern strongly contrasts with the spatial distribution of sites during the Late Pleistocene and Early Holocene, when a high

frequency of sites was found at distances between 50 and 150 km from the coast of the sea. Such distance to the coast suggests that human groups were not occupying the coast intensively. Whether these patterns are related to real population processes or are the result of supra-regional taphonomic factors related to changes in the level of the sea is a problem that requires future investigations. Moreover, some regions in the interior of the continent, as the Northeast of Santa Cruz and the North of Neuquén and South of Mendoza, have little evidence of human occupation during the Middle Holocene. The finding that the population size of Patagonia increased constantly along the from Early to Late Holocene supports the hypothesis that the lack of evidence of occupation in such areas could be related to local depopulation and human mobilization to other places rather than population extinction (Salemme and Miotti, 2008).

Other areas, by contrast, remained empty during the elapsed time since the initial peopling. This is the case for the South of Río Negro, the central area of Chubut and the center-south of La Pampa (Fig. 3). The lack of radiocarbon dates in those areas could be the result of either the lack of research or the scarcity of resources for sustaining higher population densities. The latter option is the most probable given that these areas have been as studied as others with high frequency of dates (Miotti et al., 2009; Berón, 2015), and the fact that they are characterized by a limited availability of freshwater. Particularly, the distribution of archaeological sites along the Late Pleistocene–Holocene shows that almost all sites are at less than 100 km close to the nearest river, being between 60% and 80% of sites at a shorter distance than 10 km to a permanent river (Figs. A.3 and A.4). Therefore, a strong dependence between the pattern of human occupation and the distribution of freshwater resources is observed in Patagonia.

The pattern of changes in population size and spatial dispersion since the initial peopling can be interpreted in light of the general patterns of association between population density and subsistence strategies of hunter-gatherers. Zoo-archaeological evidence suggests that the early spread of humans in southern South America was supported by the relatively high availability of large and megafauna, mainly species of *Lama* and *Rhea*, but also *Hippidion* and *Mylodon* (Borrero, 2009; Pires et al., 2016). The initial changes in population size could be related to the demographic growth of the largest survival large-herbivore, the guanaco (Pires et al., 2016). Pires and collaborators (2016) show that ca. 8000 Cal BP, after the megafaunal extinction, populations of guanacos (*Lama guanicoe*) grew fast, suggesting that the density of the humans—its main predator—was coupled with the guanaco demography. In this way, numerous evidence shows that guanaco was the main prey of Patagonian hunter-gatherers (Mengoni Goñalons, 1999; Miotti and Salemme, 1999; Pires et al., 2016). Moreover, the steepest growth during the Late Holocene period appears to be also related to the intensification in the occupation and use of resources along almost all the coast of Pampa and Patagonia.

The increase in population density (beyond a packing threshold of 9.1 individuals/100 km²) among contemporary hunter-gatherers is only observed when intensification strategies are developed, varying according to the effective temperature and the availability of aquatic resources (Binford, 2001; Johnson, 2014). It is remarkable that the packing threshold of 9.1 individuals/100 km² was probably over-passed in Patagonia during the Late Holocene. Isotopic and zoo-archaeological evidence show that the Late Holocene is characterized by a process of diversification in the subsistence strategies and diet intensification, including the incorporation of small animals and vegetables in Northwest Patagonia and South Cuyo (Gil et al., 2011; Gordón et al., 2016), the incorporation of a large diversity of aquatic resources along the coast (mollusks, fishes and pinnipeds; Zangrando, 2009; Stoessel and Martínez, 2014) and new

labour investment in food processing (Stoessel and Martínez, 2014). Particularly, an increase in the consumption of marine resources is simultaneously found between 7500 and 6000 Cal BP in different areas of the Atlantic coast, such as North of Chubut and Santa Cruz provinces, Río Negro and Tierra del Fuego (Gómez Otero, 2006; Zangrando, 2009; Favier Dubois and Scartascini, 2012; Zubimendi et al., 2015). It is worth noting that close dates were obtained here for the beginning of the demographic increase in Patagonia.

The population growth in the Middle and Late Holocene is also associated with changes in technology. Particularly, this period is characterized by the development of new technologies for obtaining (e.g. bow and arrow) and processing food (e.g. pottery and mortars; Politis et al., 2001; Stoessel and Martínez, 2014). The processes of intensification in the use of resources and technological change may have begun during the Middle Holocene (ca. 5000–4000 Cal BP) in Northwest Patagonia and South Cuyo, where domesticated plants were also incorporated (Fernandez, 1988–1990; Gil et al., 2006). In South Pampa and the Central coast of Patagonia, the process of intensification probably occurred after 3000 Cal BP (Martínez, 1999; Favier Dubois et al., 2009). In other areas, as in the coast of North Patagonia and Tierra del Fuego, the process may have begun much later, after 1000 Cal BP (Zangrando, 2009; Stoessel and Martínez, 2014). These results suggest that the processes of population growth and intensification in the use of resources were not homogeneous and simultaneous across Patagonia. Moreover, the archaeological evidence for the later Late Holocene sites is consistent with a reduction in residential mobility and the development of logistic mobility strategies (Goñi, 2010; Martínez, 2008–2009).

5. Conclusions

In sum, this study provides a well-supported pattern of the peopling and demographic evolution of aboriginal populations of Patagonia, which suggests that the colonization and posterior demographic expansion occurred earlier than generally postulated. Our results indicate a scenario in which Patagonia was peopled by small groups that arrived to the region between 17,000 and 14,000 Cal BP. At a regional scale, these populations experienced a sustained and slow growth until 7000–5000 Cal BP, when a rapid demographic expansion took place reaching its maximum at 1000 Cal BP. However, this process was not spatially homogeneous. The initial peopling followed the Atlantic and Pacific coasts, while the interior was more intensively occupied along the Pleistocene–Holocene transition and the Early Holocene. By the Middle Holocene, this trend started to be reversed and the occupation of the coast increased remarkably, while other areas remained uninhabited until the Late Holocene. The pattern outlined here, obtained on the basis of rigorous quantitative approaches, will allow the future evaluation of formal models about the ecological and cultural processes that drove the evolution of the human populations from Patagonia.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2016.05.004>.

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