Journal of Archaeological Science 65 (2016) 154–160

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: http://www.elsevier.com/locate/jas

Past population dynamics in Northwest Patagonia: An estimation using molecular and radiocarbon data

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ARTICLE INFO

Article history:
Received 15 August 2015
Received in revised form
27 October 2015
Accepted 24 November 2015
Available online xxx

Keywords:
Demography
Hunter-gatherers
Mitochondrial DNA
Radiocarbon frequency
Taphonomic bias

ABSTRACT

Studying demographic changes in past human populations is of great interest due to their role in processes of cultural change as well as the biological evolution of populations. Despite this, a general consensus about the most adequate methodological approach to this end is still lacking. Here, a new approach that combines radiocarbon frequency distributions —uncorrected and corrected by taphonomic bias— and demographic curves independently estimated with modern mitochondrial DNA (mtDNA) is used to estimate population size changes in Northwest Patagonia since the Pleistocene –Holocene transition to recent times. Results based on mtDNA sequences suggest a census size of approximately 3000 individuals (with an estimated female effective size of ca. 750 individuals) by the initial peopling of this region around 10,000 years ago. A strong correspondence between curves based on mtDNA data and those based on archaeological radiocarbon dates (n = 251) was obtained after the effect of taphonomic bias was accounted for. The demographic curves indicate that the population size was relatively stable during the earlier Early Holocene and it increased between 7000 and 5000 years ago, reaching a maximum size around 1000 years ago. Then, the population size declined until present time. We conclude that demographic inferences made on the basis of radiocarbon dates are not necessarily biased but this needs to be evaluated with independent evidence in each specific geographical region.

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1. Introduction

Understanding the demographic changes of human populations in the past has been the focus of intense research in anthropology and archeology due to their role in processes of cultural change as well as the biological evolution of populations (Bouquet-Appel, 2002; Williams, 2012). Demographic trajectories —or dynamics— of human prehistoric populations are mainly inferred from the proportion of individuals of different age classes in large cemeteries and the temporal density distribution of archaeological sites and radiocarbon dates (Bouquet-Appel, 2002; Surovell and Brantingham, 2007). The first approach is grounded in demographic expectations and it is particularly suitable to study large sedentary groups for which sites with high concentration of burials are frequently found in the archaeological record. The use of frequencies of radiocarbon dates is based on the assumption that they would be proportional to population size (Surovell and Brantingham, 2007). The main advantage of this approach is that it can be applicable to different societies, including small groups of hunter-gatherers, which usually generate a scarce and scatter record of human remains (Gamble et al., 2004; Surovell et al., 2009; Peros et al., 2010).

However, demographic estimations based on radiocarbon dates have been widely criticized because the operation of taphonomic processes could create patterns that mimic those of exponential human population growth, i.e., the higher density of later sites because of their better preservation can be confounded with an increase in population size across time (Surovell and Brantingham, 2007; Peros et al., 2010; Williams, 2012; Contreras and Meadows, 2014; Torfing, 2015a). Different methods have been proposed to correct for taphonomic bias in the distribution of radiocarbon dates using simple taphonomic expectations assuming the existence of a unique —exponential or linear, constant or variable— rate of site destruction through time in any given region of the world (Surovell and Brantingham, 2007). This is also problematic because taphonomic bias is not uniform across space and time and can be related to multiple

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http://dx.doi.org/10.1016/j.jas.2015.11.013
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factors (Allison and Bottjer, 2011). Moreover, the sample size and research strategy of archaeological sites have been recently discussed as another important source of bias for demographic reconstructions using radiocarbon dates (Williams, 2012; Timpson et al., 2015; Torfing, 2015a). More generally, because the past population dynamic is related to the radiocarbon dates by several unknown non-random factors (e.g., excavation strategies, taphonomic processes), the statistical representativeness of the sample used can be difficult to ensure (Torfing, 2015b).

The analysis of independent evidence could contribute to evaluate the presence and magnitude of taphonomic and sampling bias as well as to generate independent demographic estimations. DNA sequences of living and extinct populations provide a valuable source of information on this regard since the demographic history of a population can be inferred from signatures left in individual genomes (Ho and Shapiro, 2011). Methods developed within the framework of coalescent theory have been successfully used to estimate historical patterns of population size from the genealogy of the DNA sequences (Griffiths and Tavare, 1994; Donnelly and Tavare, 1995; Drummond et al., 2005; Fagundes et al., 2008; Mulligan et al., 2008). Despite the fact that the combined use of archaeological and molecular evidence will result in more robust estimations of past demographic dynamics, they have not been yet applied together to the discussion of temporal changes in population size in a given geographical region.

Here, we present a new approach that combines radiocarbon frequency distributions —uncorrected and corrected by taphonomic bias— and demographic curves independently estimated with molecular data from modern populations to estimate population size changes in Northwest Patagonia along Holocene. Patagonian region, in the Southern extreme of South America, was peopled by small hunter–gatherer groups during the Pleistocene–Holocene transition (Borrero, 1999; Steele and Politis, 2009). These groups inhabited a vast and nearly continuous steppe dissected by a few major rivers that flow from west to east into the Atlantic. Previous studies suggest that the occupation of this region was spatially heterogeneous and that demographic dynamics of groups inhabiting different areas were dissimilar (Borrero, 2001). This is likely related to the disparate richness and abundance of resources across the Patagonian region. Particularly the Northwest Patagonia has emerged in recent years as a region of special interest because several indicators of increased complexity and demographic growth are dated earlier there than in other areas of Patagonia (Della Negra, 2009; Perez et al., 2009; Della Negra et al., 2014; Bernal et al., 2015). These evidences comprise the presence of intentional cranial modifications, the emergence of burial areas with high concentration of individuals and the use of grinding stones around 4000–4500 years B.P, as well as the first record of pottery use with a radiocarbon date of 1878 ± 43 years B.P. However, a systematic evaluation of temporal changes in population size in this area is still lacking.

The specific aims of this study are: a) to estimate the absolute population size at initial peopling by applying Bayesian demographic techniques based on modern mitochondrial DNA (mtDNA) and use this estimation to calibrate radiocarbon curves; b) to infer changes in relative population size in Northwest Patagonia since the Pleistocene–Holocene transition to modern times by analyzing modern mtDNA data with Bayesian techniques and the distribution of calibrated radiocarbon dates corrected by the effect of taphonomic bias; c) to evaluate the similitude of the shape of growth curves obtained with calibrated radiocarbon and molecular data with the aim of obtaining a more robust estimation of the human population dynamic during the Holocene in the region of study.

2. Material and methods

2.1. Reconstructing demographic dynamics based on DNA data

Mitochondrial DNA sequences for 159 individuals from four human populations from Northwest Patagonia (Pehuenches, Mapuches from Argentina, Huiliches and Mapuches from Chile) previously studied by de Saint Pierre and collaborators (2012) were obtained from GenBank database and directly from the authors. The human sequences comprise 1016 base pairs corresponding to the mtDNA control region (rCRS positions 16032–16544 and 051–555). These sequences were aligned with MAFFT v7.012b, using the default setting (Katoh and Standley, 2013).

To investigate the demographic dynamic of human populations from Northwest Patagonia the aligned sequences of the individuals were analyzed by the Bayesian Skyline Plot method (BSP; Drummond et al., 2005), implemented in BEAST 1.6.1 (Drummond and Rambaut, 2007). This method is based on coalescent theory and relates the shape of genealogical trees —estimated with molecular data— with past population dynamics (Drummond et al., 2005; Ho and Shapiro, 2011). The Bayesian approach implemented in BEAST uses standard Markov chain Monte Carlo (MCMC) sampling procedures to co-estimate a posterior distribution of the genealogy, coalescence time and the demographic dynamics through time directly from the mtDNA sequences (Drummond et al., 2005). We used the HKY substitution model (Hasegawa et al., 1985), which was estimated using the Akaike Information Criterion with correction for sample size (AICc) implemented in Mega 6 software (Tamura et al., 2013).

The BSP analyses were performed using MCMC simulations for 50,000,000 generations and a sample frequency of 5000. Convergence was determined using the program Tracer v1.5 (Rambaut and Drummond, 2007) and the first 1250 sampled trees were excluded as burnin. The substitution rate value was defined as 3.02E-7 substitutions by site by year (Endicott and Ho, 2008; de Saint Pierre et al., 2012). We used a relaxed molecular clock model, which allows substitution rates to vary across branches according to an uncorrelated lognormal distribution (Drummond et al., 2006; Drummond and Rambaut, 2007).

We employed Tracer v1.5 (Rambaut and Drummond, 2007) to generate the BSP plot, which include average and credibility intervals —representing both genealogical and coalescent uncertainty— for the estimated effective population size at every point in time, back to the most recent common ancestor (Drummond et al., 2005). Previous to the BSP estimation, and with the purpose of identifying mtDNA sequences that are highly frequent and/or restricted to Patagonia, we plotted the genealogical tree and coalescence time obtained in BEAST using the FigTree v1.4.0 software.

2.2. Reconstructing demographic dynamics based on radiocarbon data

The radiocarbon database used in this paper contains 251 dates from different bioarchaeological and archaeological sites. It was compiled by Barberena et al. (2015) and expanded here by incorporating recently published data (Bernal et al., 2015). For sites with more than one radiocarbon date we merged those that overlapped using the informed Standard Deviation in age. In this way, we avoid possible biases generated by the intensity of research in some archaeological sites as well as differences due to unequal preservation. Using this procedure, 30 radiocarbon dates were excluded from the analyses. The radiocarbon dates were calibrated using the Calib 7.0 and the *SHCal13* Southern Hemisphere Calibration Curve (Stuiver et al., 2014). We used the calibrated radiocarbon dates in

the following analyses.

The calibrated radiocarbon dates uncorrected by taphonomic bias were graphed using a histogram to explore temporal changes. To generate this radiocarbon dates densities through time, each calibrated radiocarbon date was 'data binned' into 500-year intervals to reduce the effect of sampling bias. We repeated the analyses relaxing the assumption that archaeological sites are recovered in numbers that are exactly proportional to the size of population in the past. We first model the simplest possible taphonomic bias, where the probability that a site is destroyed by taphonomic processes remains constant through time (Surovell and Brantingham, 2007). The number of sites present at time t is $n_t = K\, e^{\lambda t}$, where n_t is the pre-taphonomic number of sites at time t in the past, λ is the constant rate of site destruction (the taphonomic rate assumed here was $\lambda = 0.0001 = 1/10{,}000$ sites destroyed per year, as suggested by Surovell and Brantingham, 2007), t is the time from the initial deposition of those sites to the present and K is the true underlying population size in the past that is a constant proportional to n_t (i.e., nt = K). Note that although the rate of site destruction is constant through time, the function used is a theoretical negative exponential distribution, which assumes an exponentially increase in the taphonomic bias through time. We also corrected the number of sites at each time t in the past by dividing the observed number of sites by the empirically derived expectative suggested by Surovell et al. (2009), where the expected $n_t = 5.726442 * 10^6 (t + 2176.4)^{-1.3925309}$. Additionally, the number of sites at each time t in the past was corrected dividing the observed number of sites by the empirically derived expectative suggested by Williams (2012), where the expected $n_t = 2.107 * 10^7 (t + 2754)^{-1.526}$. The last two expectatives are based on empirical distributions generated with a database of radiocarbon dates of volcanic deposits from worldwide (Surovell et al., 2009; Williams, 2013) and show that the taphonomic bias is higher than previously suggested by Surovell and Brantingham (2007) for older sites and that decay along time until the present. The calibrated radiocarbon dates corrected by taphonomic bias were graphed using a histogram through time.

In contrast to previous archaeological studies, the histogram of corrected radiocarbon dates was not directly used to generate a curve of relative changes in population size through time; the uncorrected and corrected radiocarbon curves were used instead to generate lower and upper boundaries of the inferred relative population changes. This approach widely used in paleontological research (Quental and Marshall, 2010) is a non-parametric and more conservative alternative to the error estimates associated to the mtDNA based curves.

We also explored the impact of type of sites as another factor that might have an effect on temporal trends of radiocarbon frequencies. We used histograms of the frequency of radiocarbon dates to compare the temporal distribution of the total number of studied sites versus open air and rockshelter plus cave sites.

2.3. Adjusting relative radiocarbon curves in absolute population sizes

Under the assumption that the frequency of calibrated radiocarbon dates is proportional to population size, the radiocarbon curves can be converted into population size using an estimated size obtained from independent data, such as mtDNA (Peros et al., 2010). Here, we used the mean Bayesian estimation based on mtDNA of the female effective population size at the early peopling of Northwest Patagonia (estimated in 10,000 years B.P.) to convert the radiocarbon curve in absolute population sizes (i.e., the density of radiocarbon dates at 10,000 B P was taken as proportional to the female effective population size at that time). The values corresponding to the lower and higher confidence intervals at 10,000 years B.P., as calculated by the Bayesian Skyline Plot method, were also used to account for the uncertainty of the estimation.

3. Results

3.1. Temporal changes in population size estimated with molecular data

The supplementary Figure A1 shows the genealogical tree and coalescence time for the complete dataset of 159 sequences. The mtDNA clades identified by de Saint Pierre and collaborators are also displayed in the figure. We also show the date for the earliest Patagonian human peopling, obtained from Steele and Politis (2009). In agreement with de Saint Pierre et al. (2012), the genealogical tree shows that all the major mtDNA clades (haplogroups and sub-haplogroups) originated locally after Patagonian peopling.

Because the early population that colonized the region might have carried an ancient demographic signal, we run the BSP using a reduced dataset that only includes the mtDNA sequences that are highly frequent and/or restricted to Patagonia. From the genealogical tree we excluded the 22 individuals displaying the basal haplogroup clades B2, A2 and D1 (Fig. A1) —mtDNA variants that are frequent in other South American regions—, while including all the Patagonian sub-haplogroups and haplotypes (e.g., B2l, C1b3, D1g1; see Fig. A1; de Saint Pierre et al., 2012). The BSP reconstruction indicates that the human population from Northwest Patagonia had a female effective population size of ca. 750 individuals during the Pleistocene–Holocene transition, and it increased after ca. 7000 years ago being more noticeable after 5000 years ago (Fig. 1; see the population size changes in log scale in the supplementary Fig. A2). The population reached an estimated female effective population size of 3500 individuals ca. 3000–4000 years ago. Then, it continued growing until reaching a size of 7000 individuals ca. 1000–1500 years ago. During the last 1000 years the human population of Patagonia steeply decreased until an estimated female effective population size of around 2000 individuals in the present time (Fig. 1). The confidence intervals generated by the BSP progressively increase from 280 to 2100 individuals by

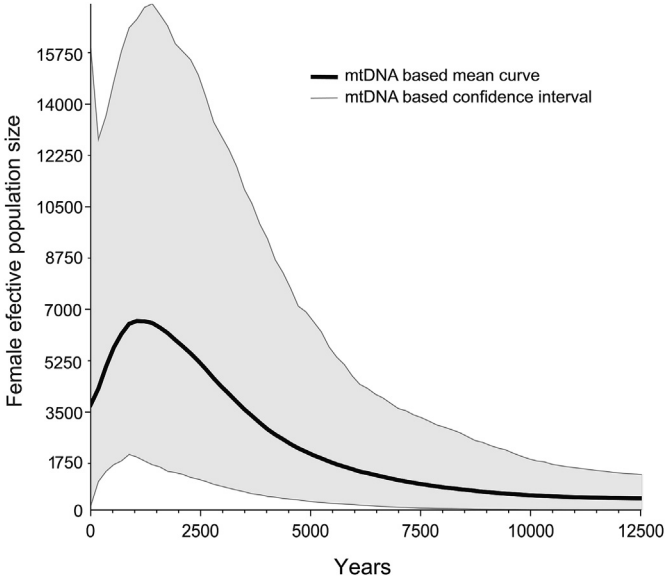

Fig. 1. BSP reconstruction of the human demographic curve based on mtDNA control region for Northwest Patagonia, using the reduced mtDNA sequence datasets.

10,000 years BP to 2000–16,000 individuals by 1000 years ago (Fig. 1). The shape of the curve estimated with the complete and reduced mtDNA datasets are similar (Fig. A1), although they differ in the time when a steep expansion of the populations is inferred (around 7500 years ago for the complete mtDNA data and 5000 for the reduced dataset).

3.2. Radiocarbon distribution plots

The Fig. 2 displays the demographic reconstruction based on calibrated radiocarbon dates using data uncorrected and corrected for taphonomic bias applying the three different methods explained above. This allows us to generate lower and upper boundaries of the inferred changes in population size through time (Quental and Marshall, 2010). The correction method proposed by Surovell and Brantingham (2007; S&B2007) results in a curve very similar to that obtained with the raw data. In contrast, the number of dates estimated after correction with Surovell et al. (2009; S2009) and Williams (2012; W2012) methods was notably higher than the uncorrected curve. Interesting, these corrections generate abrupt fluctuations in the frequency of sites than the uncorrected data, such as before and after 7000 cal BP and around 2500 cal BP. This is probable related to sampling bias of radiocarbon dates. For such reason, these fluctuations were not considered in the following analyses, interpreting only the main trend of change in the curve.

In order to make comparable the calibrated radiocarbon analyses with the molecular analyses, the frequency of archaeological sites was adjusted with a female effective population size of ca. 750 individuals at 10,000 cal BP (Fig. 3). The female effective population size for Northwest Patagonia was relatively stable during the Pleistocene–Holocene transition and grew slowly after ca. 7500 years ago. Considering our adjustment with heuristic purposes, the uncorrected radiocarbon curve suggests that population reached a size of 2000 individuals ca. 3000 cal BP and then quickly grew until a size of 8500 individuals by 1000–1500 cal BP. Conversely, the corrected radiocarbon curves by using the S2009 (and also W2012) formulas suggest that population reached a size of 2000 individuals long before (Fig. 3). During the last 1000 years the human

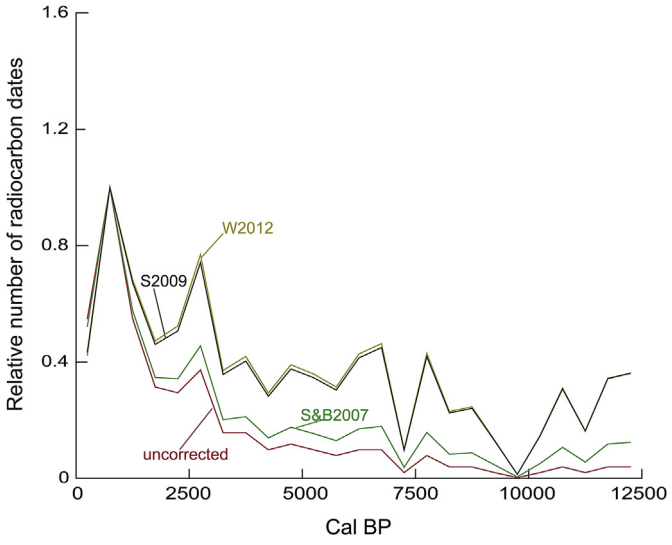

Fig. 2. Demographic reconstruction based on calibrated radiocarbon dates using data uncorrected and corrected for taphonomic bias applying three different methods, Surovell and Brantingham (2007; S&B2007), Surovell et al. (2009; S2009) and Williams (2012; W2012).

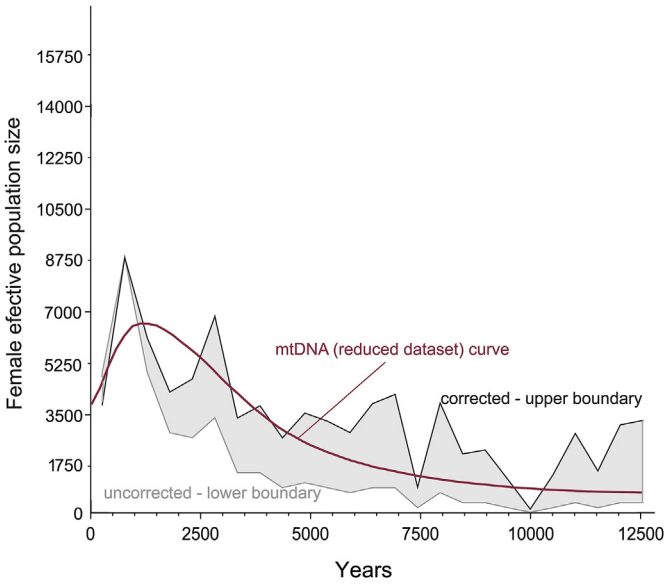

Fig. 3. Comparison of radiocarbon and molecular curves. The frequency of archaeological sites was estimated using the uncorrected and corrected calibrated dates as suggested by Surovell et al. (2009; S2009) and adjusted with a female effective population size of ca. 750 individuals at 10,000 years BP.

population of Patagonia steeply decreased until an estimated female effective population size of around 4000 individuals in the present time (Fig. 3). Interestingly, the corrected radiocarbon curves by using the S2009 and W2012 formulas generate a model of demographic trend similar to the molecular based curve (Fig. 3). However, in contrast to what was observed for the molecular data, the intervals generated by the corrected and uncorrected radiocarbon curves resulted in a relatively constant and narrower interval for the inferred population size along the period analyzed, with 1000–3000 individuals by 8000 cal BP and 7000–9000 individuals by 1000 years ago (Fig. 3). Most importantly, the interval of population size inferred with the corrected and uncorrected frequency of radiocarbon dates are within the range of the intervals estimated using the BSP confidence intervals.

Finally, the temporal trends of radiocarbon frequencies are maintained after the effect of the type of site studied is taken into account. Particularly, the distribution of rockshetler plus cave sites, which have the highest frequency in the region, display the same pattern of temporal variation as the obtained for the total dataset (Fig. A3). The open air sites display a relatively similar trend, but they represent a very low frequency along time (Fig. A3), and then have little effect in the estimated radiocarbon curves.

4. Discussion

The first question addressed here about the demography of Northwest Patagonia was the absolute size of human populations at the initial peopling. Previous affirmations about population size in this area, and more generally in all Patagonia, during the Pleistocene–Holocene transition have been highly speculative. On the basis of temporal and spatial distributions of archaeological sites and the frequency of artifacts it has been suggested that the demography was low and populations scattered, although estimations about actual sizes are not provided (Borrero, 1994–1995; Briones and Lanata, 2002; Borrero and Miotti, 2007). In this study, we provide the first estimation of the absolute population size for Northwestern Patagonian in the Pleistocene–Holocene boundary. Our results based on molecular data suggest a minimum

census size of approximately 3000 individuals (considering a female effective size of ca. 750 individuals) by ca. 10,000 years BP (Figs. 1 and 3). This estimation is slightly different to the obtained by adding the population sizes calculated for the four samples independently based on the data reported by de Saint Pierre and collaborators (2012), which results in a female effective size of 4000 individuals. Such difference could be related to the fact that the samples studied shared molecular lineages that go back to the initial peopling of the region, and thus, analyzing them separately can overestimate the population size. However, it is important to consider that the relationships between the effective population sizes estimated from the BSPs and the actual census size is complex, and therefore the conversion is a challenging problem that should be considered carefully (Eller et al., 2004). The effective population size reflects mainly the number of breeding individuals and the effects of population subdivision. The mtDNA is haploid and only passed on by mothers to offspring, and if there is not a strong population subdivision, the census size should be approximately four times greater than the effective female population size estimated with BSP analysis. However, there should surely be further corrections by factors unknown for the region under study.

It must keep in mind that estimations obtained with modern DNA data need to be interpreted with caution because they represent the surviving molecular lineages (Quental and Marshall, 2010; Molak et al., 2015). Particularly, this might be the cause of the large confidence intervals for the population size estimation, which increased from 900 to 8000 individuals by 10,000 years BP to 8000–65,000 individuals by 1500 years ago (Fig. 1). Moreover, the large confidence intervals in the mtDNA estimation could be related to well-known weaknesses of the control-region for genealogical estimation. However, our genealogical tree is in agreement with the previously established mtDNA clades (Fig. A1), as well as with the clades informed by de Saint Pierre et al. (2012), corroborating the utility of control-region at this temporal scale. There are other options to obtain more accurate population size estimations based on molecular data that need to be explored in the future. For instance, the incorporation of ancient samples could provide direct access to the extinct genealogies and allow the incorporation of these data in the Bayesian models making more robust estimates (Molak et al., 2015). Alternatively, the incorporation of genealogies of multiple and independent nuclear genomic regions can contribute to obtain better demographic estimations for human populations in the past based on a more robust molecular dataset, as it was proposed recently (Heled and Drummond, 2008).

The second question addressed here was whether the relative size of the population from Northwest Patagonia remained constant since the Pleistocene–Holocene transition to modern times. The demographic curves inferred from both molecular and radiocarbon data show a similar pattern: the relative population size was relatively stable during the earlier Early Holocene and it increased around 7000 years BP reaching a maximum size around 1000–1500 years ago (Figs. 1 and 2). During the last 1000 years the population size steeply decreased until the present time. Our analyses indicate that the initial increase in population size occurred 2000 years before the first evidence of burial areas with high concentration of individuals and grinding stones, which are found in the archaeological record around 4000–4500 years ago (Perez et al., 2009; Della Negra et al., 2014; Bernal et al., 2015). Additionally, the first record of pottery use is dated ca. 1900 years B.P., a few hundreds of years earlier than the time when the population reached the maximum size (Della Negra, 2009). Overall, these findings suggest that the demographic dynamic of human population from Northwest Patagonia was correlated with cultural changes that leave traces in the archaeological record, although they were not temporally simultaneous.

Our results show that a better correspondence between radiocarbon based curves and those based on mtDNA data is obtained after the effect of taphonomic bias is accounted for using the formulas developed by Surovell et al. (2009) and Williams (2012). As these authors point out, the non-corrected radiocarbon date distribution effectively diminish the past population size in any given time interval following a decay curve that progressively removes older evidence, and therefore the earlier estimations are more biased. An important difference between the radiocarbon curves and the molecular based curve is the existence of a larger number of fluctuations in the first ones, which could occur by chance. This problem of radiocarbon curves has been recognized in previous works, which suggested that short-term fluctuations in the observed frequency distribution of radiocarbon dates are likely a product of both real changes in human activity and chance in sampling (Surovell et al., 2009; Timpson et al., 2014). These changes at short timescales are probably related to chance when the sample size is relatively small, as in our work, and are not relevant from a demographic point of view. This problem was observed previously in the skyline methods and the more recent Bayesian approaches were developed to smooth the fluctuation and to produce a smoothing demographic function and associated estimation errors. Although we based our discussion in the long-term general trend showed by the radiocarbon curves, such as with the BSP curves, it is important that future studies develop procedures to adjust functions to the data and smooth the radiocarbon curves and associated error. Different functions, such as kernel, kriging or spline curves, could be used to smooth the distribution plot and eliminate the artificial changes in the frequency of radiocarbon dates obtained by chance.

Regarding the estimation error, the approach followed here to correct for taphonomic bias incorporates an empirical computation of error intervals in the demographic estimations, in contrast to previous studies that calculate point estimates (i.e., a single value taken as the best estimation). Importantly, the intervals of population size inferred with the corrected and uncorrected frequency of radiocarbon dates (such as is used in palaeontology; Quental and Marshall, 2010) are within the range of values computed using the BSP confidence intervals (Figs. 2 and 3). This means that the bias introduced by taphonomic processes is likely not larger than the error of palaeodemographic estimations grounded in data with a strong demographic signal (as is supported by the coalescent theory; Drummond et al., 2005) and analyzed with robust Bayesian statistical methods. These findings contrast with previous studies that suggest that radiocarbon dates cannot be considered as a good proxy of demographic changes in southern South America (Méndez et al., 2015). However, these results should not be misinterpreted, the curves of radiocarbon dates are useful for paleodemographic inference in our area of study after correcting them by taphonomic bias. However, we are not suggesting that this will be the case anywhere; for other regions or datasets, radiocarbon dates might not be a good proxy for estimating past changes in population size. The confidence of molecular and archaeological data for paleodemographic estimations need to be discussed in each case of study.

The ability to reconstruct past demographic changes using distributions of radiocarbon dates also relies on the sampling design. Previous studies have focused on the minimum sample size needed for reliable reconstructions, which was established in 200–500 dates (Michczynska and Pazdur, 2004; Williams, 2012, 2013). However, the appropriate number of radiocarbon dates is related to the extension of the geographical area and the timespan studied, and therefore, the intensity or coverage of sampled radiocarbon dates rather than their absolute number is the most relevant aspect of the sampling design. Our results suggest that 221 radiocarbon

dates appear to be sufficient in terms of intensity of sampling for a reliable estimation of the demographic changes in Northwest Patagonia. The research strategies could also have an impact over the radiocarbon curve estimation, particularly considering the type of site privileged for archaeological excavation (Surovell et al., 2009; Torfing, 2015a). The sites predominantly excavated in our region of study, rockshelter and caves (Fig, A3), have a good record probably due to the better conditions of preservation in this kind of environments compared to open air sites.

5. Conclusions

We show here that robust reconstructions of the demographic trajectory of a population can be obtained using archaeological evidence together with molecular data, and considering the problems of taphonomic and sampling bias. The methodological approach followed here provides well supported estimations of the absolute population size and the relative changes of population size in a wide timespan; two topics about the demography of past hunter-gatherers that have been largely discussed in the last years. Particularly for Northwest Patagonia, our results suggest that the founding population that colonized the region attained a size of approximately 3000 individuals by 12,000–11,000 years ago. Then, the population remained stable until 5000–7000 years ago, when an increase in size occurred, long before it was previously thought.

Overall, this study supports the premise that the temporal frequency of radiocarbon dates is a good proxy for past changes in relative population size in our region of study. Particularly, the demographic curve calculated using the frequency of radiocarbon dates corrected by taphonomic bias was widely supported by the curve estimated based on molecular sequences and Bayesian methods. In consequence, it cannot be assumed that radiocarbon dates are invariably biased but this should be tested with independent evidence in each specific geographical region. Estimations of absolute population size based on molecular data could be further improved by incorporating into the analysis sequences of ancient mtDNA and/or multiple nuclear sequences, which allows to recover lineages that might be not well represented in modern mtDNA samples.

In summary, more robust inferences of past demographic changes can only be drawn from multiple independent lines of evidence including the bioarchaeological record, modern and ancient DNA data and archaeological radiocarbon dates.

Acknowledgments

We are sincerely grateful to Sergio Furtado dos Reis (UNICAMP, Brazil) for useful discussion about historic demography and Cristina Dejean (Universidad Maimónides, Buenos Aires) for helpful comments on an earlier version of the manuscript. We thank Michelle de Saint Pierre (Facultad de Ciencias Sociales, Universidad de Chile) for providing molecular data. We are indebted to three anonymous reviewers who contributed greatly to improving the manuscript. This work was supported by grant from FONCyT ("Dinámica poblacional humana y variación en el nicho ecológico en el Noroeste de Patagonia durante el Holoceno." PICT 2014/2017–2134) and Universidad Nacional de La Plata ("Historia evolutiva y diversidad en la dieta de las poblaciones humanas de Neuquén (Noroeste de Patagonia) durante el Holoceno". 2014-2016- Nro 11/N742).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2015.11.013.

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