



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



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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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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 Tavaré, 1994; Donnelly and Tavaré, 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

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