

Domestication and human demographic history in South America

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Abstract

Objectives: The early groups of hunter-gatherers who peopled South America faced significant ecological changes in their trophic niche for a relatively short period after the initial peopling. In particular, the incorporation of cultigens during the Holocene led to a wider trophic niche and probably to an increased carrying capacity of the environment. Here, we study the relationship between the incorporation of domestic resources during the Holocene and the demographic dynamics of human populations at a regional scale in South America.

Material and methods: We employ mitochondrial DNA (mtDNA), radiocarbon data and Bayesian methods to estimate differences in population size, human occupation and explore the demographic changes of human populations in three regions (i.e., South-Central Andes, Northwest, and South Patagonia). We also use archaeological evidence to infer the main diet changes in these regions.

Results: The absolute population size during the later Late Holocene was fifteen times larger in the South-Central Andes than in Northwest Patagonia, and two times larger in the latter region than in South Patagonia. The South-Central Andes display the earlier and more abrupt population growth, beginning about 9000 years BP, whereas Northwest Patagonia exhibits a more slow growth, beginning about 7000–7500 years BP. South Patagonia represents a later and slower population increase.

Discussion: In this work we uncovered a well-supported pattern of the demographic change in the populations from South-Central Andes and Patagonia, obtained on the basis of different data and quantitative approaches, which suggests that the incorporation of domestic resources was paramount for the demographic expansion of these populations during the Holocene.

KEYWORDS

absolute population size, Bayesian methods, calibrated dates, mitochondrial DNA, population dynamic

1 | INTRODUCTION

Humans who peopled South America were hunter-gatherers that originated in the Northeast of Asia and dispersed into the subcontinent between 17,000 and 14,000 years ago (Bodner et al., 2012; Borrero, 2016; Dillehay et al., 2015; Perez et al., 2016a). The specific characteristics of this early dispersion are a long-standing topic of strong debate (Rothhammer & Dillehay, 2009). However, there is compelling evidence that for a relatively short period of time after the initial peopling the early groups of hunter-gatherers faced signif-

icant ecological and climate changes (Haynes, 2009; Larson et al., 2014; Metcalf et al., 2016).

The most significant ecological change occurred in the trophic niche of hunter-gatherers (Larson et al., 2014; Metcalf et al., 2016). Recent work suggests that there was a major megafaunal extinction about 12,000 years ago (Metcalf et al., 2016), with some species probably surviving until about 9000 to 8000 years ago (Borrero, 2009; Martínez, Gutierrez, Messineo, Kaufmann, & Rafuse, 2016). Moreover, the process of domestication of plants and animals in the Central Andes began during this period, with morphological changes indicative of full

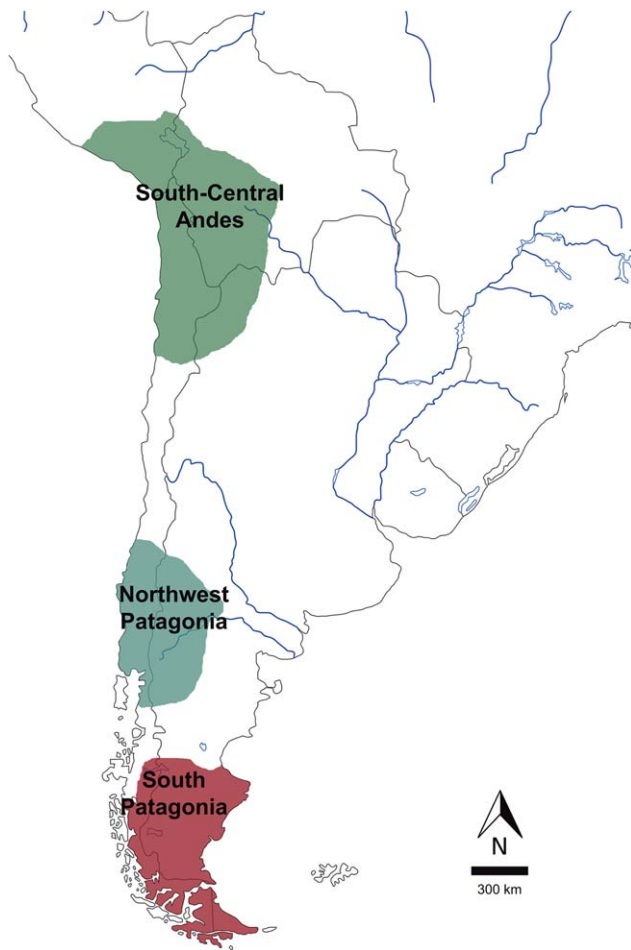


FIGURE 1 Geographical region studied in this paper

domestication already observed in several species about 6000 years ago (Larson et al., 2014). The cultigens and domestic animals expanded southward during the Middle and Late Holocene, reaching North Patagonia about 2000 to 1000 years ago (Dillehay et al., 2007; Lema, Della Negra, & Bernal, 2012; Novellino, Gil, Neme, & Durán, 2004). The incorporation of cultigens during the Holocene by the South American human populations led to a wider trophic niche and probably to an increased carrying capacity of the environment (Larson et al., 2014; Piperno & Dillehay, 2008).

These changes in the human economy could have had profound effects on its population dynamics, generating the basis for a significant demographic expansion (Boivin et al., 2016; Cohen, 1977; Larsen, 2002). There have been some recent efforts to explore the demographic dynamics of humans during the Pleistocene-Holocene in South America (e.g., Barberena, Méndez, & de Porras, 2016; Perez et al., 2016a); in some cases suggesting that the initial incorporation of domesticated resources in the region had a minimal impact on their population growth (Goldberg, Mychajliw, & Hadly, 2016). However, little is known about the real impact of the adoption of domestic resources on the demography of South American prehistoric populations (Gage & DeWitte, 2009). In particular, the ecological factors behind the demographic changes in the subcontinent have not been yet explored

adequately using quantitative approaches and considering the geographic variability in the timing and strength of domestic resource incorporation.

Here, we study the relationship between the incorporation of domestic resources during the Holocene and the demographic dynamics of human populations at a regional scale in South America. In particular, we estimate absolute population size and explore the demographic changes in the South-Central Andes, Northwest, and South Patagonia (Figure 1), three regions with populations displaying marked economic differences during the Holocene. The first two regions differ mainly in the timing and strength of the incorporation of domesticated resources into their economies, whereas the populations from South Patagonia incorporated no domestic plants or animals during the Holocene (Larson et al., 2014; Lema et al., 2012; Perez et al., 2016a). We expect that the incorporation of domestic resources had a significant effect on population growth of the South-Central Andes and Northwest Patagonia regions. We employ mitochondrial DNA (mtDNA) data to estimate the absolute population size and explore the demographic changes (Ho & Shapiro, 2011) of human populations in each region. We also employ radiocarbon data as an indirect proxy of relative changes in population size (Perez, Bernal, & Gonzalez, 2016b; Survell, Byrd Finley, Smith, Brantingham, & Kelly, 2009) and use zooarchaeological and archaeobotanical evidence to infer the main diet changes in each region. In this framework, we discuss the efficacy of both datasets, mtDNA and radiocarbon dates, for demographic reconstructions.

2 MATERIALS AND METHODS

First, we obtained 747 mitochondrial DNA (mtDNA) sequences from GenBank and previous publications (Supporting Information Table 1), corresponding to the mtDNA HVR I and II regions (ca. 1140 base pairs), from modern humans of the three regions (South-Central Andes, $N = 543$; Northwest Patagonia, $N = 148$; and South Patagonia $N = 56$) to estimate absolute population size and demographic changes in the human populations. Second, we compiled a dataset of 2992 calibrated radiocarbon dates from different archaeological sites from South-Central Andes ($N = 1616$), Northwest Patagonia ($N = 641$) and South Patagonia ($N = 735$; Figure 1; Supporting Information, Table 2) to use as an indirect proxy of relative changes in population size. This dataset was compiled in previous works (Gayo, Latorre, & Santoro, 2015; Muscio & Lopez, 2016; Perez et al., 2016a); we check for the presence of duplicated sites and eliminated dates of the same site that overlapped in the informed standard deviation. More information about the dataset can be obtained in the previous publications (Gayo et al., 2015; Muscio & Lopez, 2016; Perez et al., 2016a) and in Supporting Information Table 2.

The mtDNA sequences were aligned using the FFT-NS-2 algorithm implemented in MAFFT v7.012b, (Katoh & Standley, 2013) and used to estimate the demographic trajectories in the studied geographic regions employing the Bayesian Skyline Plot method (BSP; Drummond, Rambaut, Shapiro, & Pybus, 2005). The BSP method relates the shape

of a molecular genealogy to the demographic trajectory in the past (Drummond et al., 2005; Ho & Shapiro, 2011). The analysis was performed employing the software BEAST 1.6.1 (Drummond & Rambaut, 2007), which uses a Markov chain Monte Carlo (MCMC) sampling procedure to co-estimate genealogy, coalescence time and population size through time (Drummond et al., 2005). The analyses were run using 50,000,000 generations and a sample frequency of 5,000 for the MCMC sampling. We used the HKY model of mtDNA sequence substitution and rates of $3.02E-7$ substitutions per site per year (s/s/y; Endicott & Ho, 2008). The Bayesian Skyline plot was generated using the software Tracer v1.5 (Rambaut & Drummond, 2007). Following previous works (de Saint Pierre et al., 2012; Perez et al., 2016b), we ran the BSP analyses using all available sequences (total mtDNA dataset) or only including the mtDNA sequences that are highly frequent and/or exclusive of Patagonia (reduced mtDNA dataset).

We estimate a molecular genealogy that include modern and ancient mtDNA data to explore the possible bias in the mtDNA data because recent extinction of lineages. We employed the neighbor-joining method and the Maximum Composite Likelihood distance implemented in MEGA 7.0.20 (Kumar et al., 2016). For this analysis the modern individual sequences were combined with the ancient mtDNA published by de la Fuente et al. (2015) for South Patagonia (Supporting Information Table 1). We expect that if the extinction of mtDNA lineages in the last centuries has no significant impact in the molecular variation, all the ancient sequences will be very close to current individuals. Moreover, to test the effect of lineage extinction after the European colonization on demographic reconstruction, we estimate BSPs using alternatively modern and modern plus ancient mtDNA sequences (mainly from later Late Holocene and historical times; de la Fuente et al., 2015). It is important to remark that ancient HVR I and II regions of the mtDNA are not available for the Northwest Patagonia and South-Central Andes.

The temporal changes in the frequency of calibrated dates for each region were explored using histograms and density curves (Perez et al., 2016b; Surovell et al., 2009). The density of calibrated dates indirectly measures the human demography in a particular region. These dates were 'data binned' into intervals of 400 years to reduce the effect of sampling bias and the frequency of dates in the intervals (t) were corrected for taphonomic bias using the expectations suggested by Surovell et al. (2009), (S2009) in which the corrected value $nt = 5.726442 \times 10^6 (t + 2176.4)^{-1.3925309}$.

Finally, we described the main changes in human economy during the Holocene in the three geographical regions using the earliest date for the marine resources, domestic animals, cultigens and technology for food processing. We only considered direct evidence of the new resource based on calibrated radiocarbon dates.

3 RESULTS

The BSP plot shows that the South-Central Andes had a female effective population size of about 1000 individuals from the initial peopling until about 10,000 years ago, whereas Northwest and South Patagonia

displayed small population sizes (around 500 individuals) until 9000 and 7500 years ago, respectively (Figure 2). Population size increased slowly between 7000 and 2500 years ago in Northwest Patagonia and between 6000 and 2500 years ago for South Patagonia, reaching a female effective population size of 7000 and 3000 individuals, respectively, about 2500 years ago (Figure 2). When the total mtDNA dataset is analyzed, including individuals that probably migrated recently to the region (Perez et al., 2016b), the estimated population increase for Northwest Patagonia occurred earlier, about 8500 years ago, reaching a population size of 10,000 individuals about 2500 years ago (Supporting Information Figure 1). The population of South-Central Andes increased rapidly between 9000 and 4000 years ago, reaching a maximum female effective population size of 100,000 individuals about 2500 years ago (Figure 2).

The genealogy estimated with the Neighbor-joining method and the Maximum Composite Likelihood distance for South Patagonia is displayed in the Supporting Information Figure 2. We can observe that the modern (black) and ancient (green) mtDNA sequences are closely related, but some individuals are placed in clades that are conformed exclusively by ancient sequences (Supporting Information Figure 2). The BSPs estimated with modern plus ancient and only with modern mtDNA show a similar pattern of changes in population size along the Holocene, showing that the South Patagonia population increased slowly between 6000 and 2500 years ago. However, the female effective population size estimated for about 2500 years ago is slightly larger when the modern plus ancient mtDNA sequences are employed (Supporting Information Figure 3). The decrease in population size after about 1250 years BP is steeper when we only use modern data. These results suggest a moderate effect of recent extinction processes on the estimation of population size during the later Late Holocene.

Figure 2 displays the relative changes in population size for the three geographical regions reconstructed with the calibrated radiocarbon dates. The distribution for South-Central Andes suggests an initial peopling about 13,000 years ago, a rapid increase in the number of human occupations around 11,000 years ago, no significant changes until 7000–6000 years ago, and finally a steep increase after this date (Figure 2). In Northwest Patagonia, the evidence of the initial peopling is observed about 15,000 years ago, with low site frequency until 8000 years ago and a first growth in the number of occupations at that time and a second—more abrupt—increase after 4000 years BP. Finally, South Patagonia displays a pattern of change similar to Northwest Patagonia (K-S test = 0.214, $P = 0.251$), but the last increase in the frequency of human occupations around 4000 years BP is less abrupt (Figure 2). The distributions of dates corrected by the method of Surovell et al. (2009), (S2009) display more sudden fluctuations than the uncorrected data, mainly for South Patagonia (Supporting Information Figure 4). These fluctuations are probably attributable to biases in the sampling of radiocarbon dates, likely related to researcher interest or sampling design (Perez et al., 2016b; Torfing, 2015), and therefore we only consider the uncorrected data in the following discussion.

The three regions differ in the timing and diversity of domestic resources incorporated to the diet (Figure 3; Supporting Information,

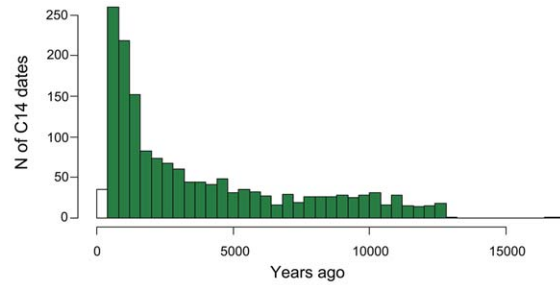
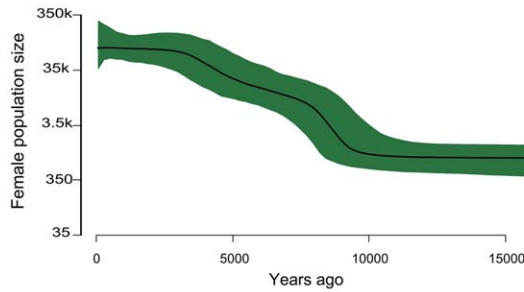
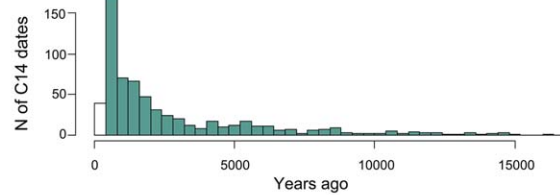
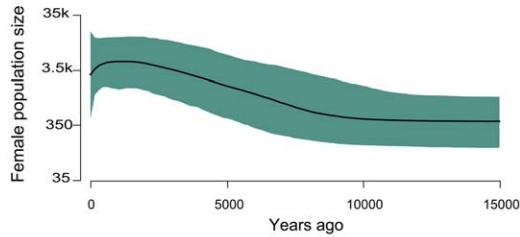
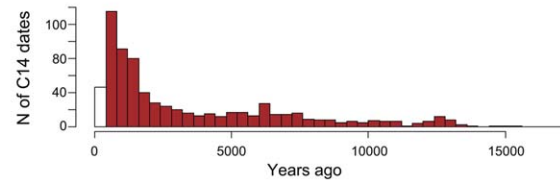
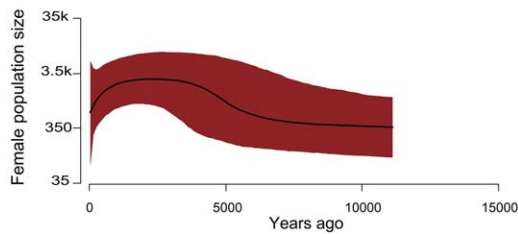
South-Central Andes**Northwest Patagonia****South Patagonia**

FIGURE 2 Demographic changes in the three studied regions estimated based on molecular curve (left) and radiocarbon (right) frequency distribution. The molecular curves were estimated including sequences that comprise the mtDNA HVR I and II regions. For the two Patagonian regions, the figure displays the BSP including the mtDNA sequences that are highly frequent and/or exclusive of each region (reduced mtDNA dataset). The frequency of archaeological sites was estimated using the uncorrected calibrated dates. Note that the decline in the presence of archaeological sites during the last 400 years BP (white bar) could be related to methodological aspects (e.g., the sites dated between 200 years BP and the present are not informed because the resolution of radiocarbon methods) or to the cultural impact of the European colonization

Table 3). In Northwest Patagonia there is evidence of the use of five cultigens and probably a domestic animal (i.e., chilihueque, possibly a domestic guanaco) between 2000 and 1000 years BP. The initial time for the incorporation of cultigens and domestic animals is more ancient, and the diversity of domestic resources is much higher in South-Central Andes than in Northwest Patagonia. At least fifteen cultigens—including corn, potato and pepo—and four domestic animals—including llama and alpaca—were present in the later Late Holocene in the South-Central Andes (Figure 3). In South Patagonia there is no evidence of domestic resources (Figure 3). The two technologies related to the processing of animals and plants, grinding tools and pottery, appeared around 10,000 and 3000 years ago, respectively, in the South-Central Andes (Figure 3). In Patagonia, the grinding tools appear 4500 years ago, whereas pottery is present about 1800 and 1100 years ago for North and South Patagonia, respectively (Figure 3). The evidences of consumption of marine resources are very ancient in the South-Central Andes, about 11,000–10,000 years BP, whereas in Patagonia these resources are present between 7500 and 6000 years BP (Figure 3).

4 DISCUSSION

In this work, we explored regional variation in the demographic trajectory of human populations from South America displaying a different proportion of domestic resources in their diets. In particular, we employed molecular data to estimate the absolute population size and the relative demographic changes during the Late Pleistocene and Holocene in South-Central Andes and Patagonia. We compared the molecular based estimations of the relative change in population size with the changes in the frequency of human occupations based on radiocarbon data. To the best of our knowledge, this is the first study that explores the differences in demography of regions with marked variation in the diet niche history and that applies a novel approach, which combines molecular and radiocarbon data.

The first topic that we will discuss here is the efficacy of both datasets, mtDNA and radiocarbon dates, for demographic reconstructions. We found global similarities in the curves estimated with mtDNA and radiocarbon dates, both show that the population density is higher

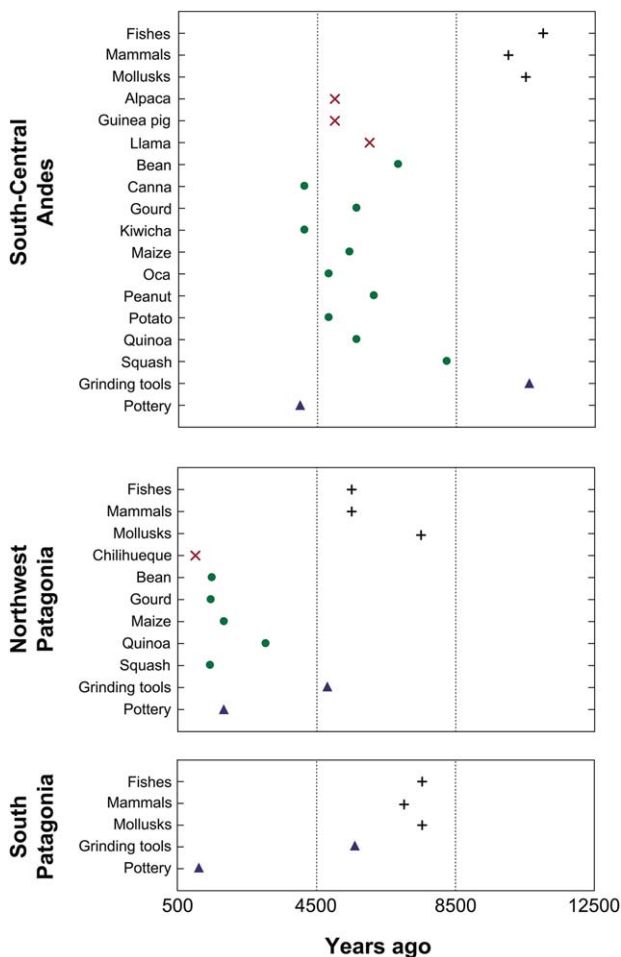


FIGURE 3 Earliest time for different economic and technological innovations in each studied geographical region

and the population growth started in the South-Central Andes earlier than in the other two regions (Figure 2). Although these results could suggest that both types of data are useful to explore main demographic trajectories in the past, the use of only one of them could bias our interpretation of the demographic changes. Particularly, the mtDNA data display a more ancient population growth than radiocarbon dates, suggesting the influence of taphonomic processes to erase the earlier demographic signal in archaeological data (Surovell et al., 2009). Previous works have suggested that this bias in the distributions of radiocarbon dates could be corrected by using specific formulas (e.g., Perez et al., 2016b; Surovell et al., 2009). However, the existence of different factors biasing the distribution of radiocarbon dates among different regions—such as researcher interest, sampling design and taphonomic processes, among others (e.g., Perez et al., 2016b; Surovell et al., 2009; Torfing, 2015)—makes difficult the use of a unique and satisfactory method to correct the curves. This could explain the unlikely pattern obtained for South Patagonia and South-Central Andes, where the highest density of occupation is observed in the late Pleistocene-early Holocene (Supporting Information Figure 4).

Contrary to the radiocarbon dates that suggest that human occupation grew at a high rate during the later Late Holocene, our mtDNA

based analyses show a stationary pattern of population size (Figure 2), suggesting the existence of some bias in the estimations based on molecular data. This dataset also suggests a marked decline in population growth during the later Late Holocene, which is estimated around 750 years BP for Northwest Patagonia and 1250 years BP for South Patagonia. These dates precede the European colonization, which was the main cause of the abrupt decrease in the size of aboriginal populations in the last five centuries, as it has been demonstrated by ancient and modern mtDNA studies (O'Fallon & Fehren-Schmitz, 2011). Because such estimations are based on mtDNA lineages, they might reflect the extinction of lineages that have had originated hundreds of years before the arrival of the Europeans. Therefore, the decline in population size during the later Late Holocene and the stationary growth are probably an indirect result of this process of lineage extinction. Interestingly, our results did not show a decline in population size in South-Central Andes even though this region was also largely affected by the process of European colonization (Figure 2).

Previous studies suggested that recent historical events had not a significant impact in the patterns of mtDNA variation in America (de la Fuente et al., 2015; Fehren-Schmitz et al., 2014; Raff, Bolnick, Tackney, & O'Rourke, 2011), with the different geographic regions displaying almost the same mtDNA variants in modern and ancient samples. However, it is important to remember that demographic reconstructions generated with modern mtDNA need to be interpreted with caution because they are based on the genealogies of the surviving molecular lineages (Molak et al., 2015; Perez et al., 2016b). This aspect can be better discussed for South Patagonia, where the impact of the European colonization was stronger and where we have relatively good samples of ancient mtDNA (de la Fuente et al., 2015). Historical data suggest that the population size of the groups inhabiting the coast and islands in Southern South Patagonia was around 8,000 individuals at time of the first European contacts and they were reduced to 300 individuals in the 19th century (de la Fuente et al., 2015). In this sense, our genealogy estimated with modern and ancient mtDNA data for South Patagonia show that all the ancient sequences are close to current individuals (Supporting Information Figure 2). Moreover, the BSP estimated with modern plus ancient mtDNA data displays slightly larger population size during the Late Holocene and a less pronounced decline in the population during the last 750 years than the estimation based on modern samples (Supporting Information Figure 2). All these results suggest that the European colonization had a significant impact at regional scale in the patterns of mtDNA variation, generating the extinction of a significant proportion of mtDNA haplotypes and causing a moderate impact on the regional demographic estimations for the later Late Holocene.

The second topic explored here is whether the differences in absolute population size among regions are related to the incorporation of domestic resources. Confirming our expectation, the population size at the later Late Holocene—about 2000–1000 years BP—was larger in populations that adopted domestic resources and generated a broader niche than in hunter-gatherer groups. Our results show that the absolute population size is fifteen times larger in the South-Central Andes

than in Northwest Patagonia, and two times larger in the latter region than in South Patagonia. Therefore, the differences in population sizes could be related to the diversity and antiquity of domestic resources in the studied regions (Figures 2–3). In particular, hunter-gatherers from South Patagonia that mainly consumed large animals, such as guanaco (*Lama guanicoe*), displayed the smallest absolute population size, while the larger populations from Northwest Patagonia and South-Central Andes incorporated a different proportion of cultigens and domestic animals into their diets (Dillehay et al., 2007; Larson et al., 2014; Martínez et al., 2016; Pérez et al., 2016a). The temperature and rainfall regimens in a large portion of Northwest Patagonia are compatible with agriculture (Johnson, Gil, Neme, & Freeman, 2015) and the evidence of the use of domestic resources, such as corn and quinoa, and cultivation on raised platforms is as ancient as 2000 to 1000 years BP (Dillehay et al., 2007; Lema et al., 2012; Pérez & Erra, 2011). However, the diversity of domestic resources and the extension of cultivation fields are larger in South-Central Andes; at least fifteen cultigens—including corn, potato and pepo—and four domestic animals—including llama and alpaca—were present in the later Late Holocene in this region (Larson et al., 2014). It is remarkable that populations from Northwest Patagonia and South-Central Andes also exploited large animals (*Lama guanicoe*; Martínez et al., 2016)—differing the importance of these animals in the diet and the proportion of alternative resources—and that in the three regions, the human groups complemented their diet with marine resources (Orquera & Piana, 2005; Santoro, Arriaza, Standen, & Marquet, 2005). Another factor that could contribute to the differences in population size among the three regions studied is the climate, especially the extremely rigorous weather characteristics of South Patagonia (Bernal, Perez, & Gonzalez, 2006).

Finally, we discuss the factors driving the population dynamics or the relative demographic changes during the Holocene. Our results show that together with the absolute differences, the three studied regions differ in the shape of the demographic curves. The South-Central Andes displays the earliest and most abrupt population growth, beginning about 9000 years BP, whereas Northwest Patagonia exhibits a more slow growth, beginning about 7000–7500 years BP. South Patagonia represents a later and slower population increase. The early population increase in Northwest and South Patagonia is not correlated with the incorporation of domestic resources but with the incorporation of marine resources in the diets, as it was previously hypothesized (Orquera & Piana, 2005). It is theoretically accepted that the diversification of resources related to the incorporation of marine animals allows the increase in population density among hunter-gatherer populations (Binford, 2001; Johnson et al., 2015). In this way, there is a large body of evidence of an increase in the consumption of marine resources between 7500 and 6000 years ago in different regions of Patagonia, together with the origin of new technologies for processing food (e.g., grinding stones) and an increase in the consumption of guanacos, all changes suggesting a significant intensification in the exploitation of animal resources (Orquera & Piana, 2005; Pérez et al., 2016a; Zangrando, 2009; Zubimendi, Ambrústulo, Zilio, & Castro, 2015).

However, the incorporation of marine resources does not explain the differences in the demographic curves between Northwest and South Patagonia. Therefore, the demographic changes observed in these regions could be related to other factors. First, these changes could be related to the incorporation of cultigens in Northwest Patagonia during the Late Holocene, about 2000 to 1000 years ago, or/and to a more diverse diet (including rodents and wild plants) in this region from the beginning of the peopling (Bernal, Perez, Postillone, & Rindel, 2016). Second, previous works hypothesized contacts between populations from Chilean Northwest Patagonia and populations from Central Andes, Central Chile and possibly Northwest Argentina (Dillehay et al., 2007), suggesting that the incorporation of cultigens during this period, together with the large population density in Northwest Patagonia, could be the result of north-south migrations. Nevertheless, at the present, there is no solid evidence for this hypothesis and future studies are necessary to better explore alternative scenarios to understand the differences in demographic history between Northwest and South Patagonia. Finally, recent studies suggest that prehistoric diets were highly diverse throughout both time and space in Northwest Patagonia, from a large variability in the use of wild animals and plants in South Mendoza and Center-South Neuquén, to the consumption of a high proportion of terrestrial animals in North Neuquén and the incorporation of an important amount of domestic resources in the Chilean Northwest Patagonia (Dillehay et al., 2007; Gordón, Perez, Hajduk, Lezcano, & Bernal, 2017). Therefore, the demographic changes observed after the Middle Holocene could be due to a complexity of factors related to the large diversity of subsistence strategies in Northwest Patagonia.

Interestingly, the rapid population growth in South-Central Andes is correlated with the adoption of an increasing number of domestic resources during the Holocene (Figures 2 and 3; Larson et al., 2014). Therefore, our results for this region are inconsistent with previous works that suggest that the demographic expansion in South America occurred before or after the origin of agriculture (Goldberg et al., 2016; Zheng, Yan, Qin, & Jin, 2012). Previous works have discussed whether the incorporation of domestic resources could have generated the basis for a major demographic expansion worldwide or, alternatively, if the demographic expansion—governed by other factors—could have driven the domestication process (Cohen, 2009; Bocquet-Appel, 2011; Weitzel & Codding, 2016). It is very likely that the adoption of domestic resources, along with the use of wild plants and animals and the use of processing technologies, generated a wider niche in the South-Central populations. These changes in the trophic niche might have contributed to increase the carrying capacity, allowing a higher population density. Recent works showed that the productivity of the first farmers not exceeded that of hunter-gatherers (Bowles, 2011). Therefore, the earlier population growth could be sustained by adding domesticated resources into the forager's diets rather than replacing them.

It is also remarkable that the use of marine resources in the South-Central Andes region is very ancient—about 11,000–10,000 years ago—and likely contributed to a rapid increase in the carrying capacity in

the region (Marquet et al., 2012; Santoro et al., 2005). In this sense, previous works suggest that there was an early demographic growth in the Pacific coast of the North of Chile and South Perú during the beginning of the Holocene, when the prehistoric human populations migrated from regions such as the Atacama inland basins toward more productive areas at the coastal valleys (Marquet et al., 2012; Santoro et al., 2005). Particularly, Marquet and collaborators (2012) suggest that cultural phenomena as the artificial mummification (known as the Chinchorro cultural complex) appeared during this period related to an increased coastal marine productivity, which caused the growth of human population size and an acceleration in the cultural innovations.

Previous works have suggested a small decline in the population size in the South-Central Andes and Northwest Patagonia about 7000–6000 years BP, related to a more arid climate (e.g., Barberena et al., 2016; Yacobaccio and Morales, 2005). Paleo-environmental studies in the Puna de Atacama show extreme aridity and high temperatures associated to a decline in the human occupations in the region between 7500 and 5000 years BP, suggesting population extinction or re-localizations (Marquet et al., 2012; Yacobaccio & Morales, 2005). Similar scenarios have been suggested for Northwest Patagonia (Barberena et al., 2016). However, we only observed a slow rate of growth in South-Central Andes about 7000–6000 years BP (Figure 2) followed by a population expansion after 5000 years ago, probably related to the development of sedentism and more intense cultivation processes, as it was recently suggested (Goldberg et al., 2016). During this period several plants and animals acquired the full domestic morphological characteristics (Larson et al., 2014), signaling the beginning of a full farmer period in South-Central Andes.

5 FINAL REMARKS

We uncovered a well-supported pattern of the demographic change in the populations from South-Central Andes and Patagonia, using mtDNA and radiocarbon data. Contrary to other datasets—such as the age composition of large cemeteries (Bocquet-Appel, 2011)—the methods based on DNA and radiocarbon data can be used to infer population dynamics in different types of populations, including small hunter-gatherer societies, and large sedentary groups (Perez et al., 2016b). These characteristics of the molecular and radiocarbon data allow the comparison of different populations and the exploration of questions about the factors behind the process of human demographic expansion, such as those formulated in this work. Moreover, the use of these two different types of evidence allows exploiting the strengths of each data. Molecular data seems to preserve information from ancient processes, while more recent events have been removed by the extinction of lineages after the European colonization. Conversely, radiocarbon dates represent relatively good evidence of the recent human occupations, where the taphonomic factors have not a significant effect; but they are not robust evidence to explore the demography in the distant past, where taphonomic plus others factors generate biased patterns.

Using these data in a combined way, our results suggest that the incorporation of domestic resources was paramount for the

demographic expansion of South American human populations during the Holocene. The differences in the demographic curve among the three geographical regions, obtained on the basis of different data and quantitative approaches, allows for a new and renovated discussion about a classical question: the relationship between the human demographic expansion and domestication (Bocquet-Appel, 2011; Cohen, 1977, 2009; Weitzel & Coddig, 2016). Contrary to recent statements (Goldberg et al., 2016), our results suggest that the domestication of plants and animals in South America was related to a relatively ancient increase in the demography of human groups. However, the importance of the incorporation of domestic resources for the population dynamic varies significantly among the studied regions. Moreover, other factors such as the early incorporation of marine resources and the increase in the rate of cultural innovation (Marquet et al., 2012) could be equally important—complementing the domestic resources—for the early demographic expansion of South American populations. Future works need to explore in more depth the temporal, spatial, ecological, and cultural complexity of the factors driving the demographic expansion in South America.

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LITERATURE CITED

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SUPPORTING INFORMATION

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