Hunter-Gatherer persistence and demography in Patagonia (southern South America): the impact of ecological changes during the Pleistocene and Holocene

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Introduction

Human populations have been exposed to significant environmental and ecological changes along their geographic expansion during the Late Pleistocene. Particularly, the changes in temperature and rainfall occurred at the end of the last glacial period impacted on the dynamics of ecological communities and spectacular changes in species richness took place (Barnosky *et al*. 2004; Haynes 2009; Lorenzen *et al*. 2011). Almost all mega-mammals and numerous large-mammals became extinct in Eurasia, Oceania and the Americas, reaching the highest extinction rates around the Pleistocene-Holocene boundary (Koch and Barnosky 2006; Haynes 2009). After the megafaunal extinction, mammalian assemblages became impoverished, although a few remaining mega-mammals survived (e.g. *Bison* and *Rangifer* in temperate North America and Eurasia; *Tapirus* and *Pecari* in tropical South and Central America; *Lama* in temperate South America) and probably became the dominant species throughout the Holocene (Haynes 2009). As a consequence, the diversity and amount of animal resources available for hunter-gatherers experienced significant fluctuations, which in turn might have induced different responses in the human groups.

Particularly, dramatic changes in the resources may have a negative impact on human population demography either because the growth rate decreases or the variance of the population growth rate increases. These fluctuations in the growth rate can generate a reduction in the population density that in the long term, and if the system does not reach a stable state again, can lead to the extinction of the population (Turelli 1978; Inchausti and Halley 2003). In this context, the persistence of the population will depend on its ability to absorb the impact of exogenous disturbances (its 'resistance') as well as on those endogenous processes that pull the demographic population parameters back towards an equilibrium (its 'recovery'). Overall, these two components determine the resilience of populations (Hogdson *et al*. 2015). Despite of its ecological and evolutionary relevance, the capacity of small hunter-gatherers populations to respond to perturbations by resisting damage and/or recovering remains largely unknown (Hoover and Hudson 2015). Investigating the causes of persistence

and the population dynamics that lead to the resistance and recovery of the system is key to understanding resilience in past human populations.

Hunter-gatherers from Patagonia (southern South America) are an excellent system for study these processes because they persisted until historical times in despite of the severe climatic and ecological changes occurred since their arrival into the region. Patagonia region was peopled around 15 000 years ago by small groups of hunter-gatherers which shared a recent and single origin (Bodner *et al*. 2012; de Saint Pierre *et al*. 2012). Palynological and glacial studies suggest that in the final Late Pleistocene climatic conditions in Patagonia were relatively warm and humid, with high primary productivity, generating a favorable environment to support a large diversity of mega-herbivores and their predators, comprising nearly 37 species (McCulloch *et al*. 2000; Tonni and Carlini 2008; Rabassa 2008; Cione *et al*. 2009). After 10 000 to 8000 years Cal BP all mega-faunal species from Patagonia went extinct, with only two large mammalian herbivores —the guanaco (*Lama guanicoe*) and huemul (*Hippocamelusbisulcus*)— surviving to the present (Borrero 2009; Cione *et al*. 2009). Archaeological evidence suggests that these large and mega-mammals, mainly the guanaco, were the main food resources of Patagonian hunter-gatherers from Late Pleistocene to 400 years BP (Borrero 2009). Despite of the fact that Patagonian hunter-gatherer groups have been the focus of numerous studies, their responses to the Pleistocene-Holocene drastic climatic and ecological changes remain largely unexplored.

Here, we will study the persistence and demographic changes of hunter-gatherer populations -as evidences of its resilience- in response to the ecological disturbances -mega-mammal extinction- in South and Northwest Patagonia region during Late Pleistocene-Holocene (Figure 1). These two areas were selected because they represent the extremes of environmental, ecological and cultural variation in Patagonia. Particularly, we will explore the relationship of the changes in population size andthe variation in faunal composition during the period under study. With this aim we will analyze molecular data of ancient and modern mtDNA employing Bayesian genealogical reconstruction and Skyline Plot methods to assess changes in the size of human populations. Zooarchaeological data will be analyzed employing measurements of individual and species abundance in order to gain insight into the ecological changes that human populations had to face in the last 15 000 years. We expect that human dynamics during the Late Pleistocene and Holocene will be correlated with the changes in the availability of resources, being strongly impacted by the mega-faunal extinction ca. 10 000-8000 years Cal BP.

Inferring the demographic history of human populations

To explore the demographic history of the prehistoric human populations from South and Northwest Patagonia (Figure 1), we analyzed mitochondrial DNA (mtDNA) sequences from descendants of aboriginal populations carrying variants (haplotypes) with high frequency and/or mainly restricted to the south of South America (Perego *et al*. 2009; Bodner *et al*. 2012; de Saint Pierre *et al*. 2012a). We obtained mtDNA sequences of 305 individuals from Northwest Patagonia and 85 individuals from South

Patagonia from previous publications and GenBank (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). The studied sequences comprise 1131 base pair (bp), corresponding to the mtDNA control region, which were aligned with MAFFT v7.012b (Katoh 2013). We estimated the model of sequence substitution using the Akaike Information Criterion with correction for sample size (AICc) as implemented in Mega 6 software (Tamura *et al*. 2013).

The mtDNA sequences were used to estimate the changes in population size along time in South and Northwest Patagonia employing the Bayesian Skyline Plot method (Drummond *et al*. 2005; Ho and Shapiro 2011). This method relates the shape of a molecular genealogy to the demographic changes of the population in the past and its algorithms are based on the coalescent theory (Drummond *et al*. 2005; Ho and Shapiro 2011). We generated the demographic curve using the Bayesian approach (BSP) implemented in BEAST 1.6.1 (Drummond and Rambaut 2007). We used a Markov chain Monte Carlo (MCMC) sampling procedures of 50 000 000 generations —sampling with a frequency of 5000 generations— to co-estimate a genealogy, time of sequence coalescence and the demographic changes through time, including average and credibility intervals –representing both genealogical and coalescent uncertainty– (Drummond *et al*. 2005). We run the analyses assuming the HKY substitution model, a rate of substitutions of 3.02E-7 by site by year (Endicott and Ho 2008; de Saint Pierre *et al*. 2012) and an uncorrelated lognormal relaxed molecular clock model (Drummond *et al*. 2006; Drummond and Rambaut 2007). The Bayesian demographic curves were reconstructed in the program Tracer v1.5 (Rambaut and Drummond 2007). We also used this software to evaluate the convergence in the MCMC simulations.

The BSP plots show that the human population from both South and Northwest Patagonia had a female effective population size of ca. 1100 individuals during the Late Pleistocene, 13 000 to 15 000 years Cal BP, and it increased slowly between 12 500 and 6000 years Cal BP, reaching an effective population size of ca. 3500 individuals (Figure 2). After this time, in Northwest Patagonia the human population steeply increased after 6000 years Cal BP until an estimated female effective population size of around 20 000 individuals by 1100 years Cal BP (Figure 2). The confidence intervals generated by the BSP progressively increase in Northwest Patagonia from 700 to 10 000 individuals by 15 000 years Cal BP to 7000-70 000 individuals by 1100 years Cal BP (Figure 2). Conversely, the population from South Patagonia grew at a constant rate, reaching an estimated maximum female effective population size of 6000 individuals ca. 1200 years Cal BP. The confidence intervals generated by the BSP progressively increased in South Patagonia from 100 to 3500 individuals by 12 500 years Cal BP to 1700-14 000 individuals by 1100 years Cal BP (Figure 2).

Reconstructing the Pleistocene-Holocene changes in trophic interactions and faunal consumption

To explore the changes in the faunal composition and diet of the prehistoric human populations, we analyzed zooarchaeological assemblages of several sites from South and Northwest Patagonia (Figure 1). These sites were dated between the Late Pleistocene and late Holocene periods (Miotti and

Salemme 2003; Borrero 2009; Prates *et al*. 2013; Perez *et al*. 2016; Table 1). Only cave sites with a long sequence of occupation and zooarchaeological assemblage of large sample sizes were included in this study. Because we only used cave sites, a general similarity in the depositional environment for all assemblages is ensured. This is particularly relevant due to the differences in the presence and incidence of taphonomic agents between caves and open air sites (Surovell *et al*. 2009; Torfing 2015). Moreover, caves in Patagonia are in general the only sites that sampled the whole chronological range for human occupation, from the Late Pleistocene to the Late Holocene. For the North region we studied six caves, while for the South region 10 caves were included (Figure 1, Table 1). Total faunal sample comprises 37 850 specimens, 15 826 from Northwest Patagonia and 22 024 from South Patagonia.

First, we analyzed the changes in the diversity of species in the assemblages, enumerating the species observed and estimating the Shannon diversity index (Shannon 1948). For assessing temporal changes in diversity, we obtained data on the number of species for different temporal strata in the studied archaeological sites. Changes in the species diversity along time are the most direct estimation of the impact of ecological disturbances on the human population dynamics. Second, we studied the changes in the size of the faunal assemblages throughout time, as an indirect measurement of the changes in the intensity of animal consumption. For this, we obtained data for the number of identified specimens (NISP; Lyman 2008) of faunal species for different temporal strata in the studied archaeological sites. The size of the faunal assemblages was calculated as the sum of the NISP of the different sites for each temporal stratum. Third, we estimated the proportional changes in the main prey exploited by humans in Patagonia, *Lama guanicoe* (Borrero 2009). We measured the relative frequency of guanaco over other faunal species using the NISP guanaco/NTAXA index (number of species; Grayson and Delpech 1998). We also estimated the minimum number of individuals (MNI; Lyman 2008) for each stratum because this measure is more robust than NISP/NTAXA when the assemblages are fragmented (Grayson and Delpech 1998). Additionally, we obtained an alternative estimation of the relative frequency of guanaco by dividing the NISP of this species by the total NISP of the stratum, obtaining percentage values (% NISP). This allowed us to estimate the relative importance of guanaco in the diet of the prehistoric human populations compared to the other potential prey used by them. The temporal changes in the species diversity, the size of faunal assemblages and the relative contribution of guanaco to the human diet was explored plotting the Shannon index, NISP and the NISP guanaco/NTAXA against the mean time of each stratum.

The Figure 3 displays the temporal changes in the Shannon diversity index. A decreasing pattern in the Shannon values is observed from the past to the present times, for both the Northwest and South Patagonia, being stronger in the former. In both regions, during the Pleistocene-Holocene transition the diversity of species was higher as a result of the presence of extinct taxa (*Mylodon sp.*, *Dusycionavus* and deer extinct in the Northwest, and *Lama gracilis*, *Hemiaucheniaparadoxa*, *Hippidionsaldiasi*, *Mylodon sp.*, *Megatherium sp*., *Pantheraoncamesembrina* and *Rheaamericana*in the South). Moreover, the values of Shannon index are higher in the Northwest than in South of Patagonia along all the studied period, indicating a greater diversity of species used in the first region. In the case of Northwest Patagonia taxa

as dasipodidos, fish, flightless birds, mollusks, carnivores (felines, canids and mustelids) and rheids were exploited, while in the South the range of species is smaller. These results are concordant with the higher species diversity expected for North Patagonia, since species diversity decreases with increasing latitude (Willig *et al*. 2003; Adams 2010). However, this greater availability does not explain the difference in slopes of the tendency lines between the two regions. In Northwest Patagonia more species are always included in the assemblages, but their presence also decreases more rapidly, while in South Patagonia, after the process of extinction of megafauna, diversity remained is contained within narrower limits with less variation throughout the Holocene.

Figure 4 displays size changes of the assemblages in the two studied regions. Total quantity of osseous specimens assigned to different species displays a general increase from the Pleistocene-Holocene transition to the late Holocene in both regions. However, a significant increase, together with gaps, is observed in the middle Holocene in both regions. In this sense, the first great increase in the size of the assemblage is observed in Northwest Patagonia during the Late Pleistocene, followed by a relatively stable pattern until the Late Holocene. In South Patagonia the first increase in the size of the assemblage is observed ca. 10 000 Cal BP.

The proportion NISP guanaco/NTAXA shows that the contribution of guanaco to the assemblages grows over time in the two areas (Figure 5). It should be noted that the consideration of other measures of abundance, such as the MNI or NISP guanaco/total NISP (results not shown), display a similar pattern. However, the pattern of relative increase in the guanaco contribution is stronger in South Patagonia. Moreover, it is interesting to note that the guanaco is more important during the Pleistocene-Holocene transition in Northwest Patagonia than in the South region. In this regard, there are several sites with extinct fauna in South Patagonia but only one with evidence of human exploitation of megafauna in the Northwest. This absence of remains of megafauna could be due to differences in the sampling effort in each area, problems of preservation or the absence of suitable habitats for megafauna. Finally, the increase in the contribution of guanaco to the total NISP is more marked in South Patagonia, as is shown by the tendency line.

Relating demographic dynamic with the ecological changes along the Pleistocene-Holocene

The analyses of faunal assemblages of archaeological sites from Northwest and South Patagonia show a clear trend towards a decrease in the diversity of species consumed from the Pleistocene-Holocene limit to 8000-7000 years BP, remaining relatively stable after that date. This pattern is probably related to the decrease in faunal diversity as a consequence of the extinction of mega-mammals initiated 12 000 years ago. The available evidence suggest that unlike other regions, such as in North America where most species went abruptly extinct, in Pampa and Patagonia the process was gradual and spanned around 5 000 years (Hubbe *et al*. 2007; Borrero 2009; Prates *et al*. 2013). Overall, our results agree with previous studies indicating that as the faunal diversity decreased, subsistence practices of hunter-gatherers changed. Previous studies have interpreted the reduction diversity in faunal assemblages as a change from generalist to more specialized subsistence strategies (Miotti and

Salemme 1999; Prates *et al*. 2013). However, if we consider the decrease in diversity along Late Pleistocene and Early Holocene, it is clear that Holocene human populations consumed the surviving species, mainly the guanaco (Cione *et al*. 2009; Novaro 2010; Pires *et al*. 2016). These changes can be understood in the frame of processes favoring ecosystem stability, e.g. the adjustments in species densities maintaining overall community biomass. These processes can reinforce the resistance of the ecological community to disturbance, as well as of its constitutive populations, and thus favor stability and persistence (Connell and Ghedini 2015). Interestingly, the amount of biomass consumed by human populations in Patagonia, as measured by the NISP, grew at a constant rate throughout the Late Pleistocene until the Late Holocene. Such inverse relationship between diversity of species and biomass suggests that hunter-gatherers not only consumed a progressively smaller number of species, but that these species were more intensively exploited. Whether the increase in the number of specimens was associated to an intensification in the exploitation of anatomical elements with lower return needs to be further explored.

Despite of the sustained decrease in faunal diversity, the size of human populations, as estimated by molecular data, displayed a consistent positive trend throughout the Pleistocene-Holocene in both geographic regions although with some differences. In Northwest Patagonia, the rate of population growth displayed a notable acceleration around 7000-6000 years BP, when the diversity of faunal resources consumed reached a stable value. Similar changes in the human population growth of Northwest Patagonia have been previously documented on the basis of radiocarbon frequency distributions uncorrected and corrected by taphonomic bias (Perez *et al*. 2016), suggesting that the demographic pattern observed in our results is robust. The ecological factors underlying the human population growth after the Early Holocene have not been thoroughly discussed yet. According to our results, these changes in population size cannot be fully explained considering the changes in faunal resources only since the rate of increase in faunal biomass is lower in this region than in South Patagonia. Given the higher diversity of ecological settings at lower latitudes, which are supported here by higher diversity of fauna in Northwest than in South Patagonia, hunter-gatherers from Northwest Patagonia might have broadened their niche by incorporating resources other than fauna. In this sense, Carbon and Nitrogen isotope values of human remains suggest the incorporation of vegetables to the diet of these groups since 7000-6000 years BP (Fernandez and Panarello 2001; Gordón *et al*. 2016). The use of vegetables is also supported by the high concentration of grinding stones in the archaeological record of Northwest Patagonia around 5000-4500 years ago (Perez *et al*. 2009; Lema *et al*. 2012; Della Negra *et al*. 2014; Bernal *et al*. 2016). Another technological change that might be related to a broad niche is the use of pottery, which was first used at least 1900 years ago (Della Negra 2009), a few hundreds of years earlier than the time when the population reached the maximum size. These technological innovations might have contributed to food processing (grinding and cooking), resulting in the incorporation of a larger quantity of nutrients (Carmody *et al*. 2011).

In South Patagonia, the demographic growth is associated to an increase in the faunal biomass that seems to be dominated by the consumption of guanaco. Previous studies have shown that the

population of guanaco had a sustained growth after 8000-7000 years BP, which might have been favoured by the gradual occupation of the geographical areas previously dominated by mega-mammals (Pires*et al.* 2016), a compensatory process that allows ecosystem stability. Accordingly, isotopic and zooarchaeological data suggest that South Patagonian hunter-gatherers based their diet in faunal resources, being the guanaco the main prey throughout the Pleistocene-Holocene (Borrero 2009; Tessone*et al*. 2009). Along with the increase in importance of guanaco in the diet, several technological changes took place. Particularly remarkable is the predominant use of stone balls around 8,000 to 6,000 years BP, a hunting technology used until historical times (Cardich*et al*. 1973). The incorporation of stone balls, a thrown weapon, during the middle Holocene allowed a greater weapon repertory for the hunting of large-herbivores who survived to the extinction, such as guanaco and ñandú. It is worth noting that the first evidence of grinding tools and pottery are found thousands of years later in South than in Northwest Patagonia, and they seemed to be used for meat instead for plant processing (Cassiodoro and Tessone 2014; Pallo and Borrero 2015). This further supports the stronger dependence on hunting of southern populations, which in turn might account for the slower growth and the lower density attained by these populations. Other indirect evidence related to a decline in mobility and an increase in population density, such as the presence of formal burial areas, are also dated later in South than in Northwest Patagonia (2000 and 5000 years BP respectively; Della Negra *et al*. 2009; García Guraieb *et al*. 2015; Perez *et al*. 2016), providing independent evidence in line with the results reported here.

Final remarks

In summary, our study suggests that hunter-gatherers from Northwest and South Patagonia were resilient to the significant ecological changes that took place during the Late Pleistocene and Early Holocene. Particularly, the rate of population growth was not impacted by -i.e. was resistant to- the reduction in the diversity of available resources as a consequence of mega-mammal extinction around 10 000-8000 years Cal BP. The resistance of hunter-gatherers from Northwest and South Patagonia could be related to the ability of human populations to absorb the impact of relatively slow ecological changes, as was the extinction of mega-mammals in Patagonia. The chronological association between the demographic dynamics and some archaeological evidence suggests that cultural responses (i.e. technological changes) might have contributed in some extent to maintain and even increase the human population density. Despite of the similarities between the two regions, the human populations responded in different ways to the extinction of a significant number of the animal species consumed and also displayed different demographic trajectories. While in South Patagonia the population persisted through a low but constant rate of growth that followed the demographic growth of its main prey, the Northwest population showed a faster rate of growth probably sustained by an increase in the carrying capacity of the environment mediated by cultural changes.

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Legends for figures and tables

Figure 1 . Map showing the geographic localization of the archaeological sites analyzed

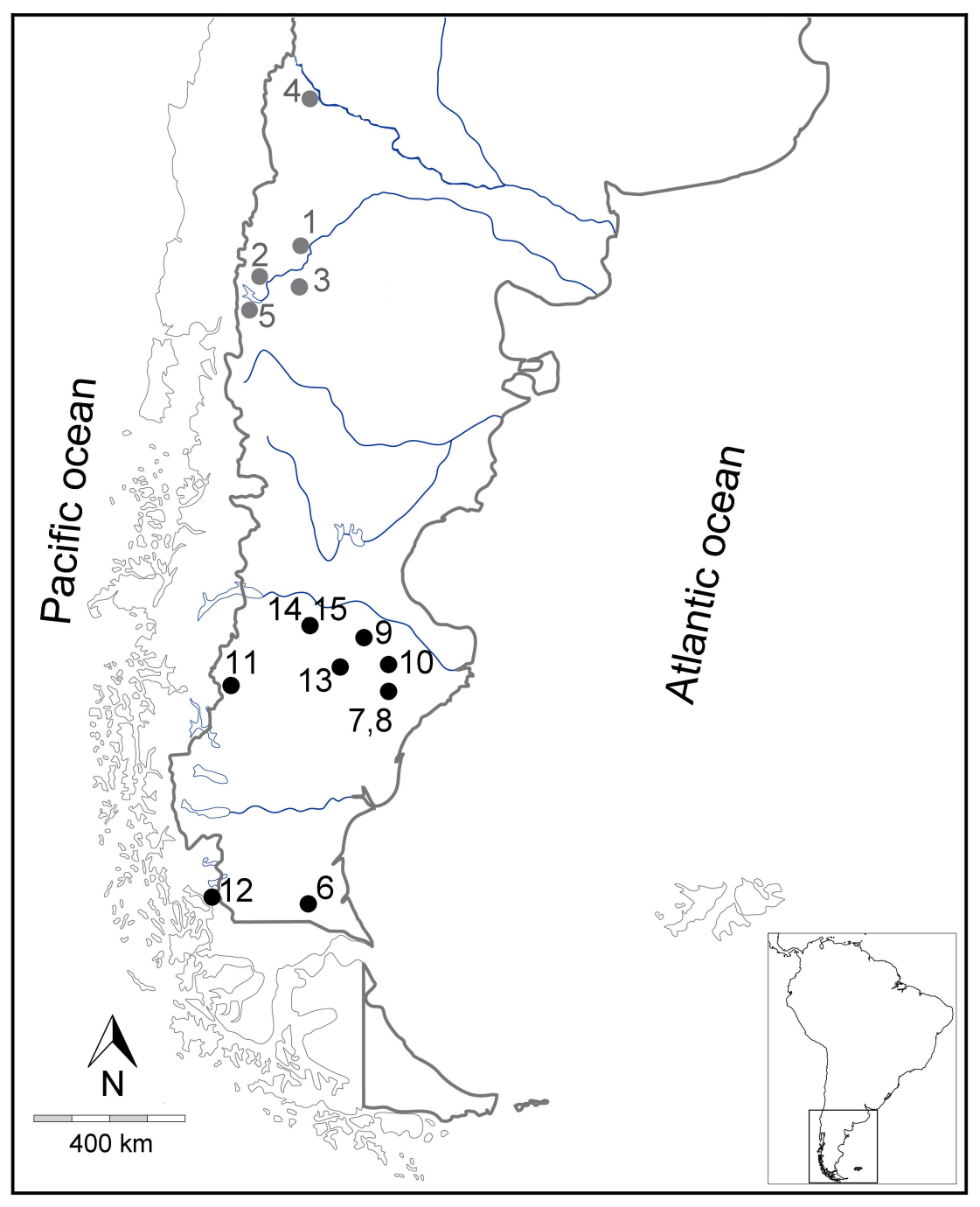
Figure 2. BSP plots for human populations from Northwest and South Patagonia

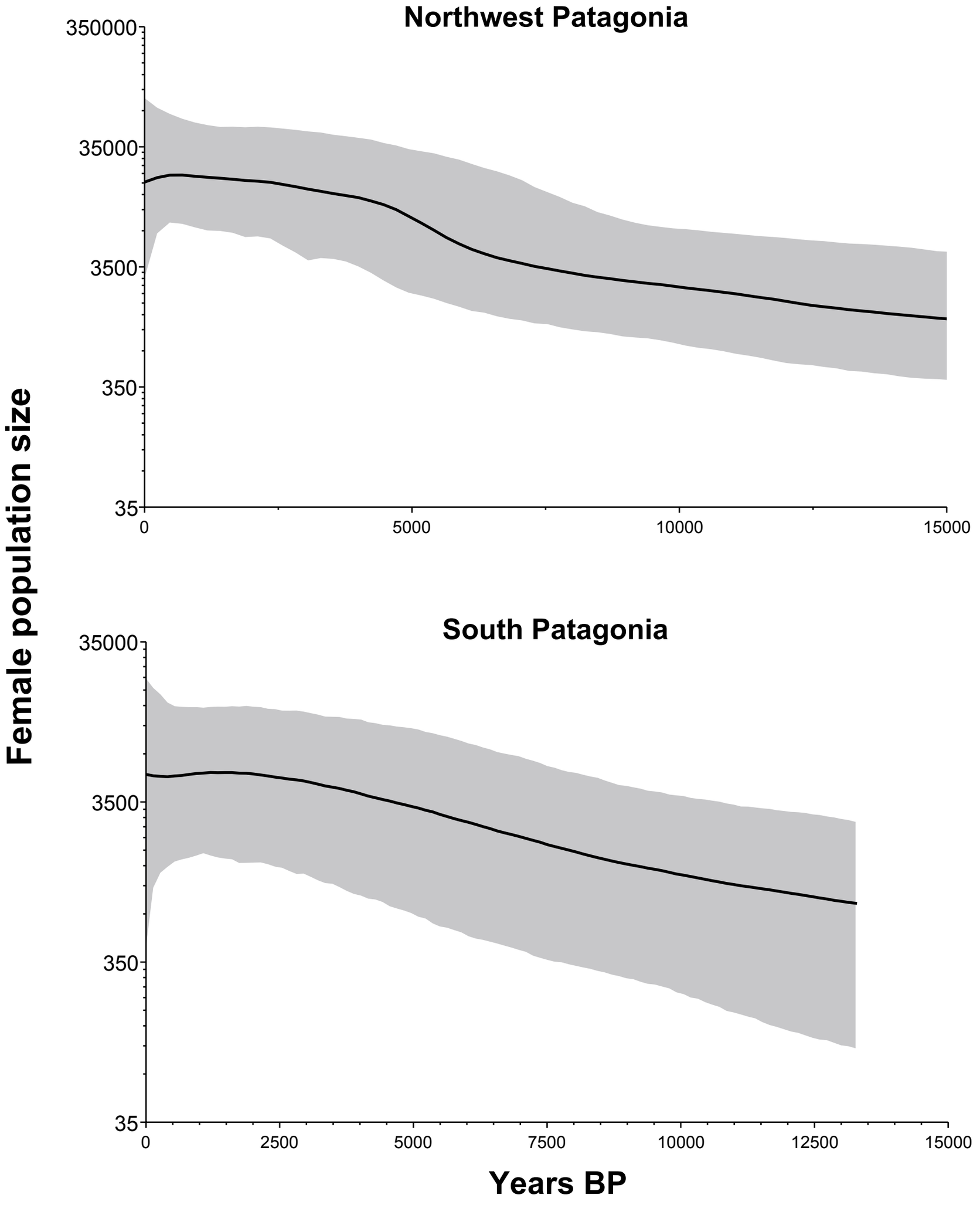
Figure 3. Temporal changes in the Shannon diversity index for the faunal assemblages from Northwest and South Patagonia

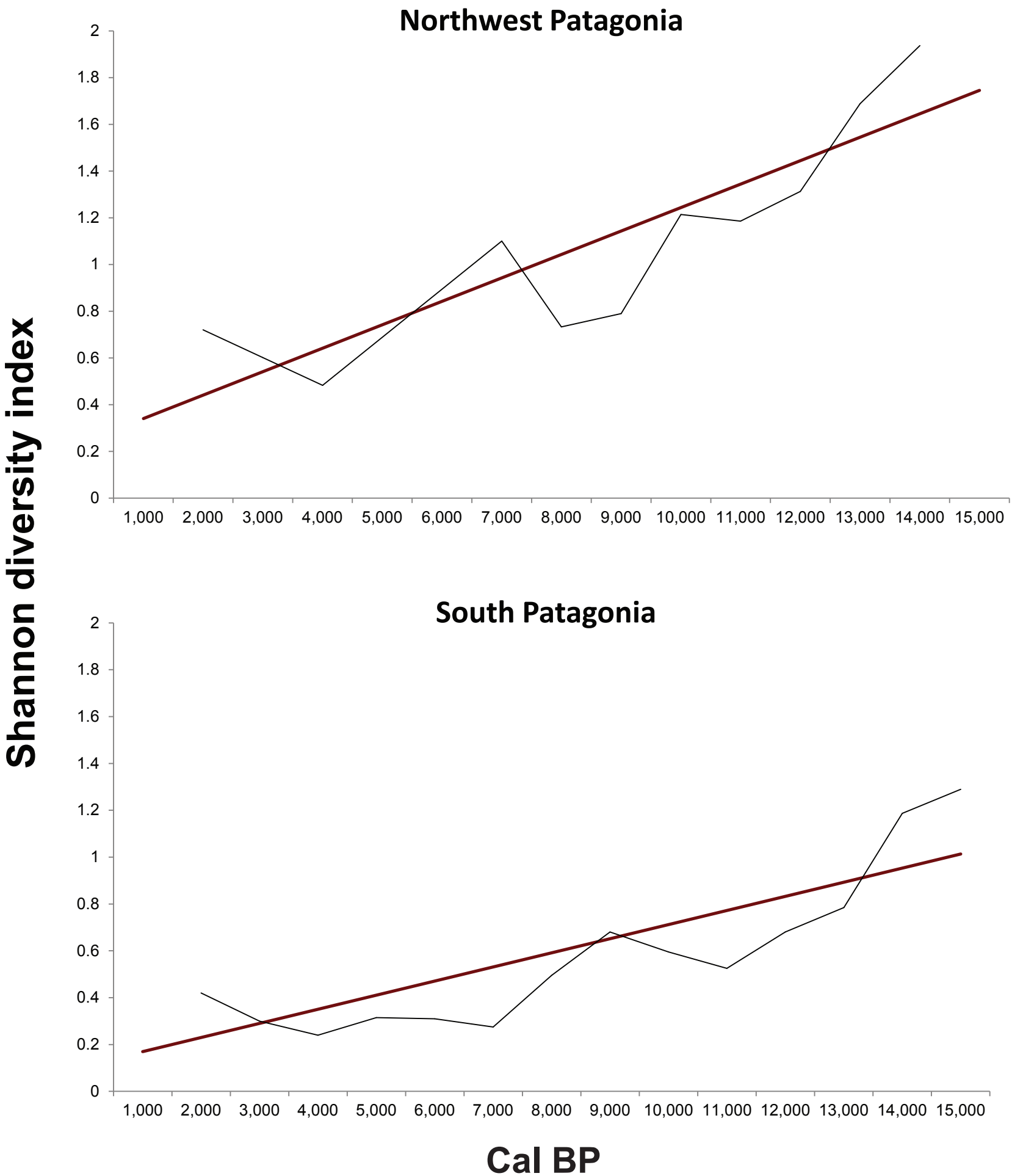
Figure 4. Temporal changes in the size (NISP) of faunal assemblages from Northwest and South Patagonia

Figure 5. Proportion NISP guanaco/NTAXA over time in the two geographic areas studied

Table 1. List of archaeological sites from Northwest and South Patagonia studied in this work


Pacific ocean
Atlantic ocean
4
1
2
3
5
14
15
9
11
13
10
7,8
12
6
N
400 km


Northwest Patagonia
350000
35000
3500
350
35
0
5000
10000
15000
South Patagonia
35000
3500
350
35
0
2500
5000
7500
10000
12500
15000
Female population size
Years BP


Northwest Patagonia
South Patagonia
Shannon diversity index
Cal BP
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
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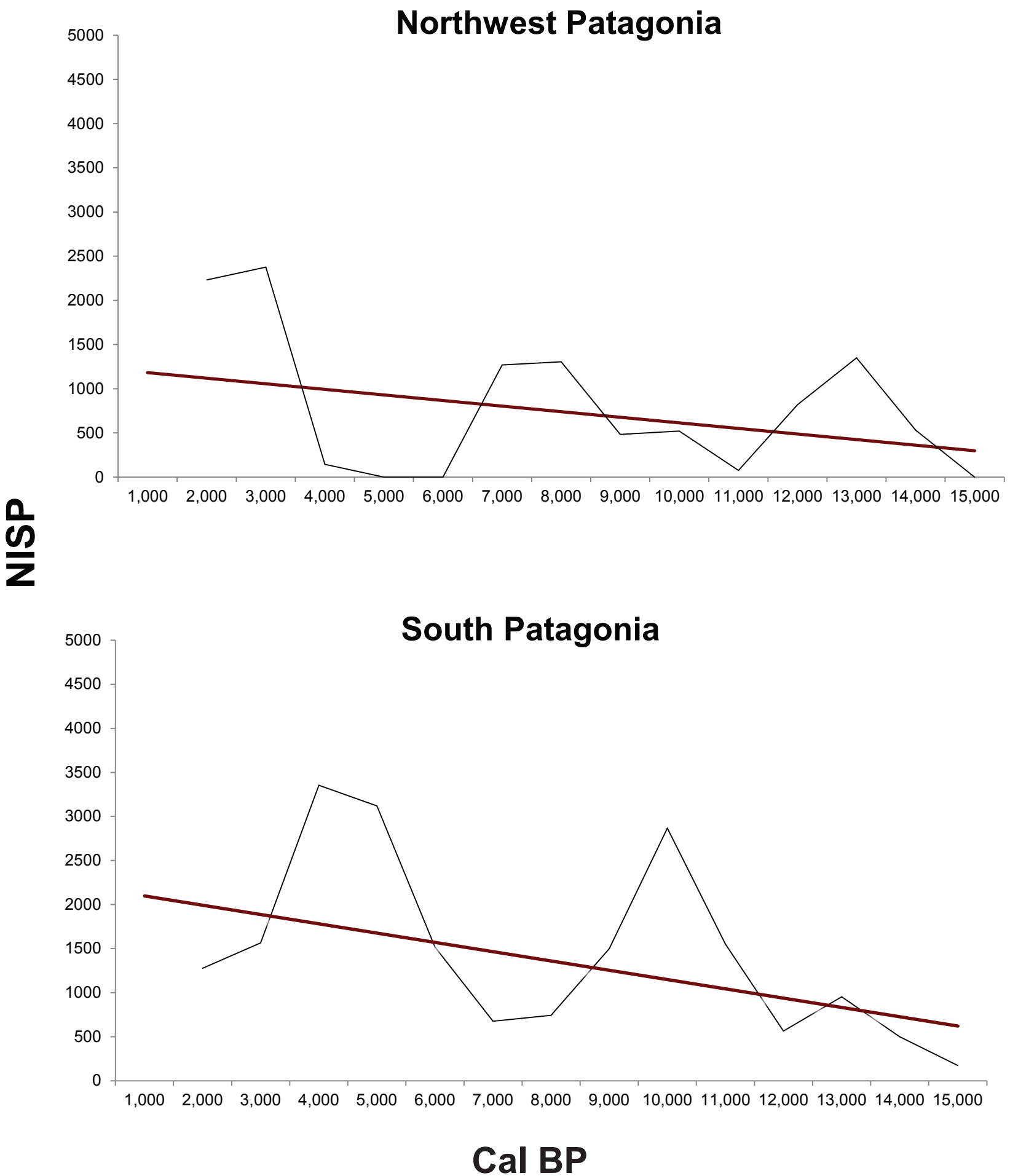
13,000
14,000
15,000


Northwest Patagonia
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
11,000
12,000
13,000
14,000
15,000
NISP
South Patagonia
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
11,000
12,000
13,000
14,000
15,000
Cal BP

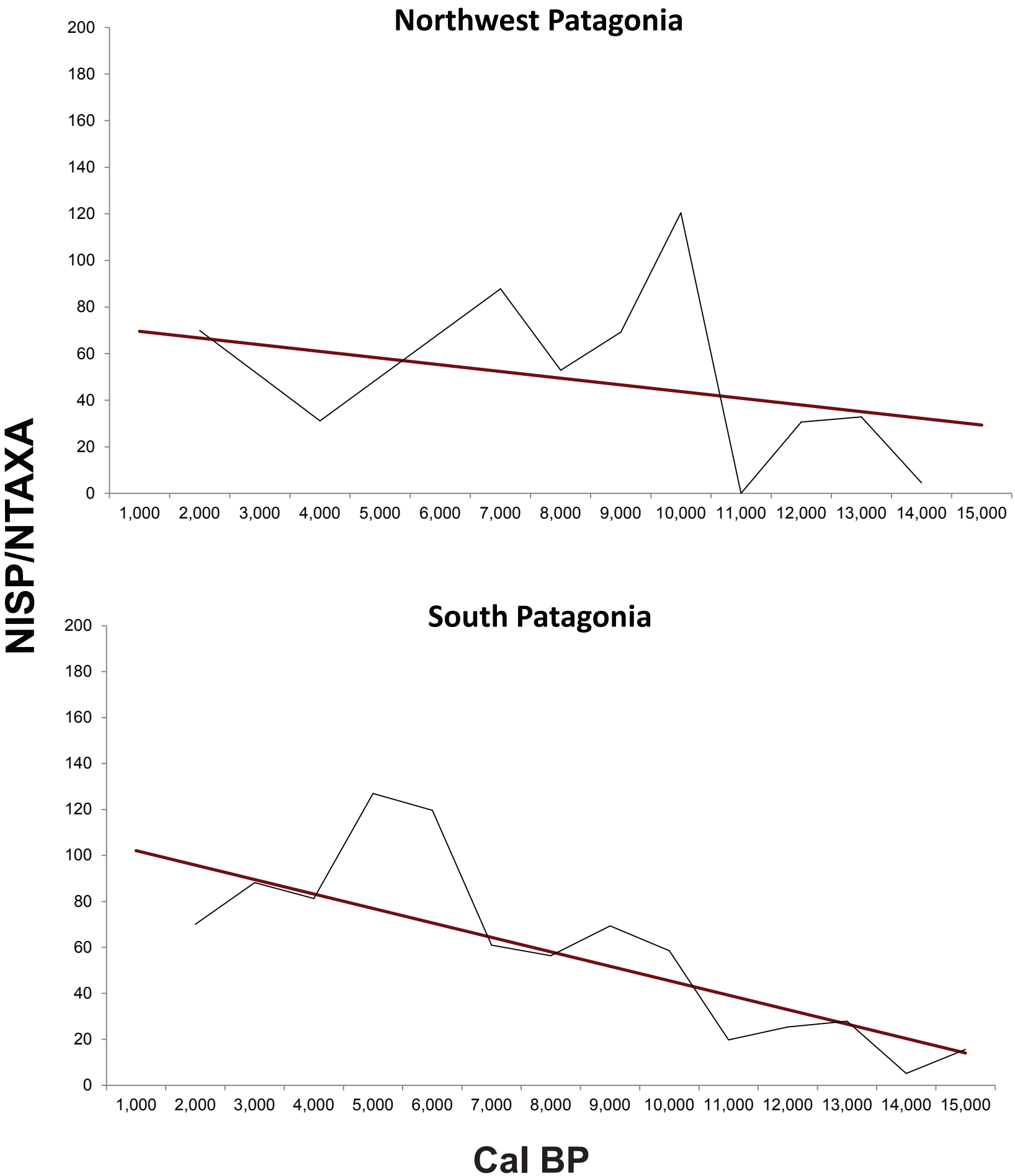

Northwest Patagonia
South Patagonia
NISP/NTAXA
Cal BP
200
180
160
140
120
100
80
60
40
20
0
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
11,000
12,000
13,000
14,000
15,000

Table 1. Archaeological sites studies in this work.

Region	Site	Map reference	Reference
Northwest	Cueva Epullán Grande	1	Cordero 2009, 2010
	Cueva Traful	2	Cordero 2010, 2011
	Cueva and Paredón Loncomán	3	Cordero 2007, 2010
	Cueva Huenúl	4	Barberena *et al*. 2015
	Cueva El Trébol	5	Lezcano *et al*. 2010
South	Cueva Fell	6	Emperaire *et al*. 1963
	Cueva Tunel	7	Paunero *et al*. 2005
	Casa del Minero	8	Paunero *et al*. 2007
	Cueva 3 de Los Toldos	9	Cardich *et al*. 1973
	Piedra Museo	10	Miotti 1996; Marchionni 2013
	Cerro Casa de Piedra 7	11	De Nigris 2004
	Cueva del Medio	12	Nami and Menegaz 1991
	Cueva Maripe	13	Marchionni 2013
	Cueva de las Manos	14	Mengoni Goñalons and Silveira 1976
	Cueva Grande del Arroyo Feo	15	Silveira 1979