

South Central Andean Area. Social Interaction, Relationship and Genetic Divergence in the Atacama Desert

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Abstract

Social relations and their impact on genetic divergence are analyzed between localities in a key path linking the Argentine Northwest with the Northern Arid of Chile. The study was carried out with 1168 individuals from the sites of Puna de Jujuy, San Pedro de Atacama, Calama, Pisagua and 29 craniometric variables. Discriminant Analysis methods were used for the evaluation of differences between sites and sexes and the reclassification of individuals in another site than the original one. The F_{st} statistic was calculated to determine the genetic structure and the kinship relationships within and between populations. The F_{st} value between localities is $F_{st}=0.0825 \pm 0.0030$. Considering the sexes by site, the observed genotypic variance ($F_{st}=0.1195 \pm 0.0037$) increased by 45%, compared to the expected variance. The Puna de Jujuy sample showed a greater contribution of outside the region variability, including both sexes, in relation to the remaining sites. The migratory effect between localities depended mainly on the circulation of men and by a smaller proportion, the women. Migration rates estimated between localities vary between 1.8 and 2.8 individuals per generation. Evidence of extinction of kinship by distance between localities is presented. There is also evidence of patterns of matrilineal residence.

Keywords: exchange, social relations, integration and genetic divergence.

1. Introduction

Archaeological research revealed the occupation of the Central South Andean Area (CSAA) from 13000-12000 BC and the development of different stages, periods or phases that explain the evolution of society and the interaction between different sub-areas through 500 generations. In northern Chile, human occupation by groups of hunters and gatherers has been recorded for 13000 years (cal BP) (Grosjean et al., 2005; Latorre et al., 2013; Núñez et al., 2002, 2010) and in the Argentinian Puna, between 12500 and 10000 years (cal BP) (Yacobaccio, 2017). Interaction between different regions included transhumance and caravan activity with the traffic of goods and the transit of people through a complex network of roads and routes that connected localities and regions of Peru, Bolivia, Northern Chile (NCH) and Northwest Argentina (NOA) to historical times (De Nigris, 2009; Llagostera, 1995; Molina Otárola, 2011; Montenegro & Ruiz, 2007; Nielsen, 2002, 2011; Núñez & Dillehay, 1995; Tarragó, 1977, 1984; Yacobaccio, 2012). The activity of caravans must have influenced the local genetic composition by reproduction between individuals from different localities and lineages (e.g. migratory effect) (Lecoq, 1987; Nielsen, 1997-1998, 2013). It has been suggested that the migratory movements recorded in the 17th century from the Atacama region for various causes (commercial traffic, emigration of families and men for working purposes) to different geographical areas including the NOA, could reflect activities and customs existing in pre-Hispanic times (Difrieri, 1980). In the NCH, in San Pedro de Atacama, migrant individuals were detected based on the markings established by the $^{87}\text{Sr}/^{86}\text{Sr}$ concentration at Coyo-3, Coyo Oriental, Solcor-3 and Larache (Knudson et al., 2012; Torres Rouff et al., 2015).

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A witness case about the residency of foreigners was found in this locality by the discovery of four female skulls in a tomb with evidence of injuries from Leishmaniasis, an infection acquired in trans-Andean areas (of North-Eastern Argentina or in Southern Bolivia) and possibly related to exogamous marriages (Costa et al., 2009; Costa & Llagostera, 2014). The relationships between regions of the CSAA were derived by exploring in time and space the influence of genetic drift and migration on the genetic composition of populations. For example, between South Bolivia, NCH and NOA (Cocilovo et al., 2009; Varela et al., 2008, 2013, 2014) and between cultural periods of San Pedro de Atacama (Varela & Cocilovo, 2009, 2011). The experience provided a more realistic explanation of regional evolutionary history and stimulated the development of studies between localities linked to South-Andean traffic. Recent works have analyzed the magnitude of the interactions between the Puna de Jujuy, San Pedro de Atacama and Calama (Cocilovo et al., 2017; Fuchs et al., 2016b).

The study of the relationships between these localities provided important information that enabled evaluation of the genetic divergence and association between different lines of evidence with the conditional probability (Bayes' Rule) of individuals belonging to one locality or the other (Cocilovo et al., 2017). The results obtained prompted the current research in order to explore the properties and characteristics of the relationships between localities on the route that connects both slopes of the Andes Mountains to the Pacific Ocean coast. These locations are part of a caravan route that was important for human development and social integration in the CSAA due to the relationships between NCH, NOA, southern Peru, Bolivia and Tropical Forests.

Based on phenotypic traits, it is possible to determine the relations of kinship and the magnitude of the migratory effect on the divergence of the populations of Puna de Jujuy, San Pedro de Atacama, Calama and Pisagua in the period from 300 BC to 1400 AD. This study includes the analysis of the extinction of kinship with the distances between localities and their relationship with the regional evolutionary process. It also explores the possible existence of gender-based residence patterns of individuals.

2. Material and Methods

The research of the regional diversity was made from the analysis of craniometric measurements in the following stages: 1) Description of the available samples from each locality, 2) Analysis of the composition of each locality in terms of sex and artificial deformation, 3) Characterization of the mean phenotypes and evaluation of the differences between localities, 4) Analysis of the reclassification of the individuals in their own group or in a different one, 5) Analysis of the differences between the sexes by locality, 6) Analysis of the genetic divergence and estimation of migration rates and 7) Analysis of the correlation of the different statistics both among themselves and with the distance between localities. The samples come from the ancient cemeteries of NOA (Puna de Jujuy) and NCH (San Pedro de Atacama, Calama and Pisagua) (Figure 1).

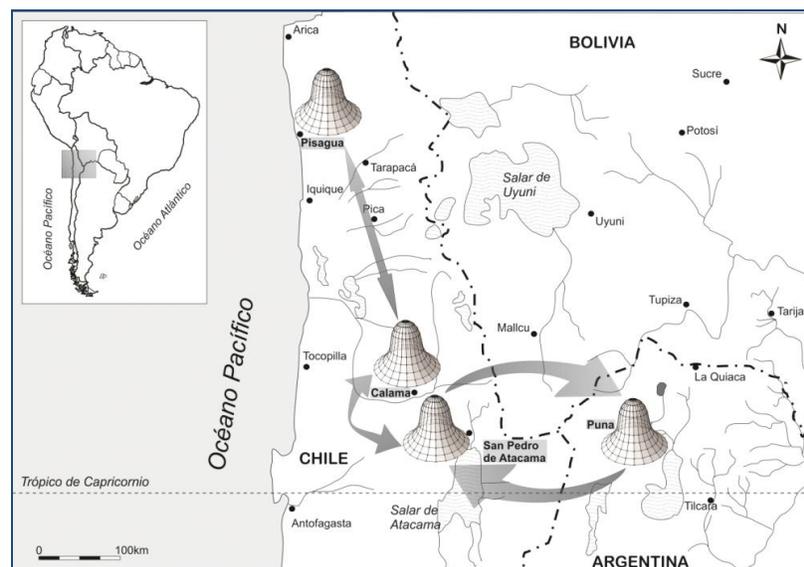


Figure 1: Location of the Puna de Jujuy, San Pedro de Atacama, Calama and Pisagua

The Puna de Jujuy (PUJU) is a vast territory of the NOA on the eastern slope of the Andes mountains range of 30000 km² and an altitude of 3700-4400 meters above sea level. It has a warm and humid climate in the north and temperate and dry in the west and south. The earliest settlement was recorded in 13000 AP (Yacobaccio, 2017). The materials used in this study were obtained at sites of the Late Period (Agua Caliente, Casabindo, Doncellas, Queta, Río Negro, Sorcuyo and Tablada de Abra Pampa) with dates in the interval of 964 ± 45 AP (cal d.C 1029-1208 $\pm 2\sigma$) for the Pucará de Rinconada and 501 ± 42 AP (cal d.C 1400-1497 $\pm 2\sigma$) for Casabindo (Fuchs, 2014; Fuchs & Varela, 2013) and they are conserved in the Museo Etnográfico “Juan B. Ambrosetti”, Universidad de Buenos Aires) and in the Museo de La Plata (Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata).

To the west of the PUJU, across the Andes, approximately 398 km in the arid north of Chile, San Pedro de Atacama (SPAT), an important oasis, is located at 2436 meters above sea level. It has a desert climate with high solar radiation and great daily thermal amplitude. In this locality was an extensive cultural development from the Arcaico period (between 7810 and 4110 BC, Núñez & Moraga, 1978) until the Spanish conquest. SPAT includes a series of tombs with funerary contents of the local and foreign material (Llagostera, 1995; Llagostera et al., 1988; Tarragó, 1977, 1984, 1989). The materials corresponded to individuals buried in various places between 300 BC and 1532 AD, preserved in the Museo Arqueológico “R. P. Gustavo Le Paige” from San Pedro de Atacama, Chile.

The Calama locality (CALA) is 101 km to the NW of SPAT, on the shores of the Loa River 2200 meters above sea level, with a desert and cold climate. In a sector of the village, seven km south on the left bank of the Loa River (Cárdenas, ms) is the Chunchuri site dating from 1390 AD (Dupont-1 site) from the Late Pre-Inca period (Núñez, 1965, 1968, 1976; Núñez et al., 2003; Núñez & Pimentel, 2008). The materials were collected by Max Uhle between 1912 and 1913 (Cocilovo et al., 2016; Durán et al., 2000) and are conserved at the National Museum of Natural History in Santiago, Chile.

On the arid coast of the NCH, 550 km from SPAT is the site of Pisagua (PISA) which also has a desert climate and abundant cloud cover. It has a continuous record of occupation from the VIII millennium BC until the Spanish conquest (Núñez, 1965, 1980). The bone remains were obtained by Max Uhle between 1912 and 1913 and are conserved at the National Museum of Natural History in Santiago, Chile. They correspond to cemeteries associated with three stages of the agro-pottery period (Formative, Middle Late and Regional Development) in the interval between 300 BC and 1450 AD, during which there is an active interaction between the local society and other more distant subareas (Agüero 2009, ms; Cocilovo, 1994; Cocilovo et al., 1999; Quevedo & Cocilovo, 1994, 1995).

The study of population structure and relationships between localities was based on the analysis of 1168 individuals from PUJU (329), SPAT (624), CALA (161) and PISA (54). The sample consisted of individuals of both sexes, of adult, mature and senile age with and without artificial deformation of the skull. The determination of sex, age and artificial deformation was carried out in accordance with Genovés (1962), Dembo and Imbelloni (1938) and Buikstra and Ubelaker (1994). Twenty-nine metric variables (Table 1) were obtained in accordance with Bass (1981), the Convención Internacional de Mónaco (1906) and Wilder (1920) using original instruments from Siber and Hegner (Switzerland).

Table 1: Craneometric variables

Maximum cranial length	Basion-prosthion length	Palate length
Maximum cranial breadth	Nasion-prosthion height	Palate breadth
Basion-bregma height	Nasal height	Orbito-alveolar height
Porion-bregma height	Nasal breadth	Foramen magnum length
Minimum frontal breadth	Cheek height	Foramen magnum breadth
Maximum frontal breadth	Biorbital breadth	Sagittal curve nasion-bregma
Upper facial breadth	Orbital breadth left	Sagittal curve bregma-lambda
Bizygomatic breadth	Orbital height left	Sagittal curve lambda-opistion
Bimaxillary breadth	Maxillo-alveolar breadth	Horizontal curve
Basion-nasion length	Maxillo-alveolar length	

The sex distribution of each locality made it possible to assess social and labor differences related to the management of local resources and the exchange of foreign products by the llama caravans within the scope of the SCAA. The analysis of the deformed cranial types by locality made it possible to analyze relations at the regional level and to infer a process of social integration due to the coexistence of different customs, traditions and identities.

The phenotypes of each locality, of both sexes and of each sex by locality were analyzed using multivariate statistical methods: MANOVA and Discriminant Analysis (Seber, 1984). The correlation among D^2 values between sites with geographical distances and the D^2 correlation between sexes for each locality was analyzed. In addition, the classification of individuals into their own group or a different group was determined by the associated conditional probability according to the Bayes' Rule (Montes Suay, 2007). These calculations allowed the establishment of: 1) the homogeneity of each sample, 2) the distribution of the cases assigned to a different group from the original one, 3) their relationship with the D^2 values, 4) their association with sex and 5) the relationship with the geographical distance and the chronological periods determined by archaeology.

The population divergence was determined by the F_{st} statistic for quantitative traits according to Relethford (1994, 1996, 2001 and 2002), Relethford and Blangero (1990), Relethford and Harpending (1994) and Relethford et al., (1997). The F_{st} statistic measures the magnitude of genetic differentiation from the relationship of mean variance within and between populations (Varela & Cocilovo, 2000, 2002). This relationship varies according to the balance between the effect of genetic drift and migration in the absence of selection and mutation. However, F_{st} is relatively insensitive to the influence of these factors (Slatkin, 1994). Relethford (1994) demonstrated the comparability of information provided by quantitative traits and genetic markers. In a case study with anthropometric characters, Konigsberg and Ousley (1995) showed that the genetic variance-covariance matrix is proportional to the phenotypic variance and covariance matrix ($\mathbf{G} = h^2 \mathbf{P}$). The impact of the environment on inter-population assessments was relativized by Sparks and Jantz (2002) demonstrating the absence of plasticity in the human skull. In addition, it has been proven in a wide range of global populations that neutral processes were more important than climate in determining the shape of the human skull (Betti et al., 2010). Finally, according to the work of von Cramon-Taubadel (2014), craniometric data can be reliably used to study the history of ancient populations, dispersion models and affinities between populations.

Genetic drift tends to decrease genetic variation within populations and increase divergence, while migration tends to produce greater genetic homogeneity among them. The effect of the genetic drift can be compensated by the migratory flow from nearby or distant localities with the contribution of genetic novelties that favor the increase of the local genetic variability. The F_{st} statistic was calculated with a heritability (h^2) of 0.55, an acceptable value according to Relethford (1994), Relethford and Harpending (1994) and previous experience for the study in local populations of the maximum genetic variance of quantitative characteristics (Medeot et al., 2008; Varela & Cocilovo 1999, 2007) according to Falconer and Mackay (1996). RMET program version 5.0 was used

(<http://employees.oneonta.edu/relethjh/programs/>).

For the F_{st} statistics estimation, the following experimental designs were considered: 1) general between locations, 2) between locations for each sex, 3) between sexes by locations and 4) correlation analysis of independently calculated F_{st} values between the male and female sexes of each locality. Based on this information, the magnitude of the regional gene flow and that coming from a source external to the studied region was estimated. These predictions are based on the calculation of the migration rate per generation of Sewall Wright's original development: $Nm = 1/4 * [(1/F_{st}) - 1]$. In addition, the spatial layout of the localities was used to calculate migration, assuming a model based on stepping-stone. In this model the effect of migration depends on distance and is evaluated from the estimator $M = 4Nm/k$, where k is the distance between populations (Slatkin, 1994). These calculations made it possible to assess the impact of the global and sexes migration effect on genetic divergence between populations and the reproductive behavior of individuals at local and regional levels, according to Konigsberg (1988).

3. Results

The distribution of sex in the total sample (Table 2) revealed a majority of male individuals (59%). The proportion of both sexes is similar in SPAT and men are more frequent in PUJU (66%), CALA (72%) and PISA (65%). The differences are statistically significant (% of the total of each locality: $X^2 = 34.6$, $df = 3$, $p < 0.001$). Differences in the distribution of the types of artificial deformation of the skull were also found ($X^2 = 249.9$, $df = 9$, $p < 0.001$). Between the different localities, the frequencies of non-deformed individuals are similar and different types of deformities coexist. Oblique tabular shapes (OT) predominate in PUJU and erect tabular shapes (ET) in SPAT. The different types of deformation have similar frequencies in CALA and circular (C) frequencies predominate in PISA (Table 3).

Table 2: Distribution of the sample by sex

Localities	Sex		Total
	Male	Female	
Puna de Jujuy	217 (66)	112 (34)	329
San Pedro de Atacama	319 (51)	305 (49)	624
Calama (Chunchuri)	116 (72)	45(28)	161
Pisagua	35(65)	19 (35)	54
Total	687 (59)	481 (41)	1168

$\chi^2= 34.6$, $df=3$, $p<0.001$; the percentages of the total of each row are indicated in parentheses

Table 3: Distribution of the sample with and without artificial deformation by locality

Localities	Deformation	Erect	Oblique	Circular	Not Deformed	Total
		Tabular	Tabular			
Puna de Jujuy		20 (6)	170 (52)	19 (6)	120 (36)	329
San Pedro de Atacama		259 (42)	127 (20)	37 (6)	201 (32)	624
Calama (Chunchuri)		44 (27)	35 (22)	35 (22)	47 (29)	161
Pisagua		10 (19)	10 (19)	18 (33)	16 (30)	54
Total		333 (29)	342 (29)	109 (9)	384 (33)	1168

$\chi^2= 249.9$, $df=9$, $p<0.001$; the percentages of the total of each row are indicated in parentheses

There are significant phenotypic differences between localities (PUJU, SPAT, CALA and PISA), (Wilks' Lambda: 0.219 approx. $F_{(87,3399)}=25.81$, $p<0.001$). Figure 2 shows the distribution of each group according to the first three discriminating coordinates that accumulate 87% of the total variation. The Mahalanobis D^2 statistic also indicates significant differences between pairs of localities (Table 4) and these values correlate with the spatial distances between the samples of each locality (Figure 3) (correlation coefficient: $r=0.94$, $p<0.05$).

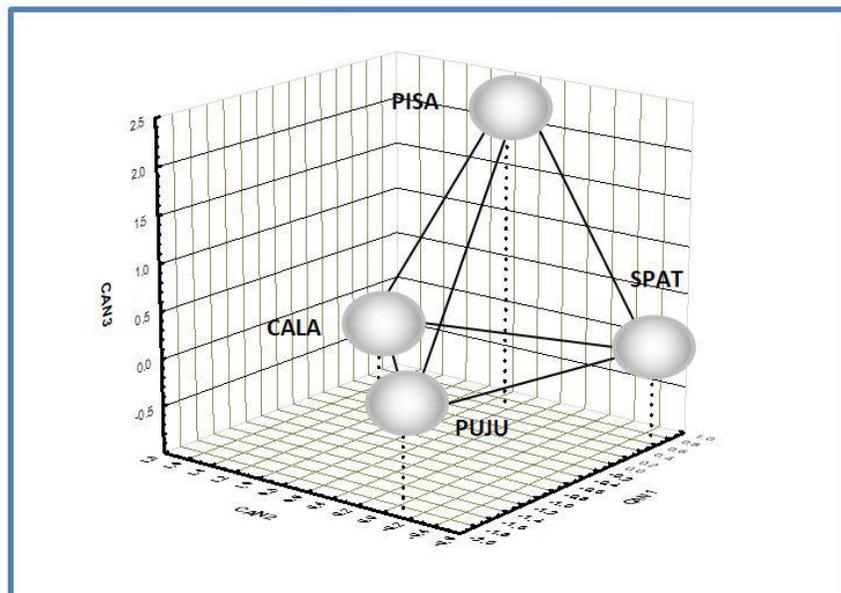


Figure 2: Location sites by the discriminant coordinates I, II and III (87.3% explained variance). Mean canonical variables. PUJU: Puna de Jujuy; SPAT: San Pedro de Atacama; CALA: Calama (Chunchuri) and PISA: Pisagua.

Table 4: Mahalanobis distance. Differences between mean phenotypes of the localities

Localities	Puna de Jujuy	San Pedro de Atacama	Calama (Chunchuri)	Pisagua
Puna de Jujuy	0.00	6.90	9.09	12.33
San Pedro de Atacama	6.90	0.00	4.81	7.05
Calama (Chunchuri)	9.09	4.81	0.00	8.34
Pisagua	12.33	7.05	8.34	0.00

Global difference: Wilks's Lambda: 0.219 approx. $F_{(87,3399)}=25.81$. For all cases $p<0.001$

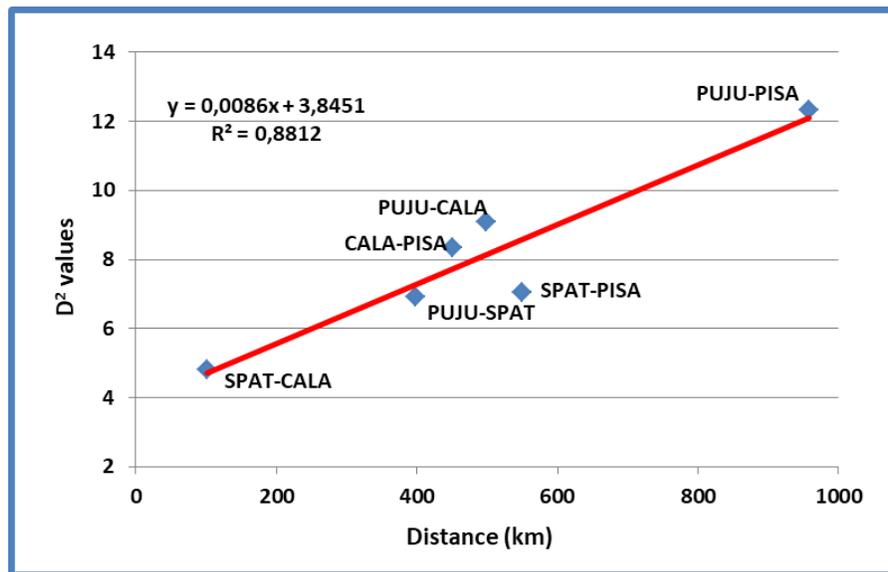


Figure 3: Distribution of sites according to D² values and distances between sites in km ($r=0.94$, $p<0.05$). PUJU: Puna de Jujuy; SPAT: San Pedro de Atacama; CALA: Calama (Chunchuri) and PISA: Pisagua.

The analysis of the reclassification of individuals by the greater probability of being assigned to one location or another indicated that 84% were classified to the group itself and 16% to another one (Table 5). Table 6 shows the percentage of individuals reclassified in a different locality and the average probability for each case. The highest number of individuals from other localities assigned to SPAT (51% of the cases: 96/187) is noted. In addition, the highest proportion of male reclassification occurred between SPAT, CALA and PUJU and the proportion of female reclassification decreased from east to west, from PUJU to the remaining localities (Figure 5). In general, 84% of reclassified individuals are adults and matures.

Table 5: Reclassification of cases. Estimated ranking in columns

Localities	Correct Percentage	Puna de Jujuy	San Pedro de Atacama	Calama (Chunchuri)	Pisagua	(*)
Puna de Jujuy	85.1	280	39	9	1	14.9
San Pedro de Atacama	89.9	36	561	21	6	10.1
Calama (Chunchuri)	66.5	8	40	107	6	33.5
Pisagua	61.1	0	17	4	33	38.9
Total	84.0	324	657	141	46	16.0

(*): Percentage assigned to another group

The radial graph in Figure 6 highlights the proportion of cases reclassified by period among the different localities. An increasing proportion of individuals were assigned from any place to the Early (3%), Middle (25%) and Late (72%) periods. The highest reclassification was in the Late Period between PUJU, SPAT, CALA and PISA and in the Middle Period between SPAT, PUJU and CALA.

Table 6: Percentage and average probability of individuals reclassified between locations

Localities	Indexes	Puna de Jujuy	San Pedro de Atacama	Calama (Chunchuri)	Pisagua
Puna de Jujuy	%	-----	11.9	2.7	0.3
	$\bar{p} =$		0.11	0.03	0.01
San Pedro de Atacama	%	5.8	-----	3.4	1.0
	$\bar{p} =$	0.06		0.06	0.02
Calama (Chunchuri)	%	5.0	24.8	-----	3.7
	$\bar{p} =$	0.05	0.18		0.02
Pisagua	%	0.0	31.5	7.4	-----
	$\bar{p} =$	0.03	0.13	0.05	

Total of reclassified individuals: 187 (16%)

Table 7 shows the analysis of the sex differences based on D^2 values for each locality. All paired comparisons are statistically significant ($p < 0.001$) as well as the overall difference (Wilks' Lambda: 0.092 approx. $F_{(203,7736)} = 15.98$, $p < 0.001$). In all cases, the magnitude of sexual dimorphism and the increasing value of the differences between the sexes in relation to distances among localities (Figure 10) from CALA-SPAT to PISA-PUJU are highlighted. The diagram in Figure 4 shows the D^2 (Ward method) values between sexes by locality where the consistency of the expression of the mean phenotypes of both sexes and their greater differentiation in PISA is observed.

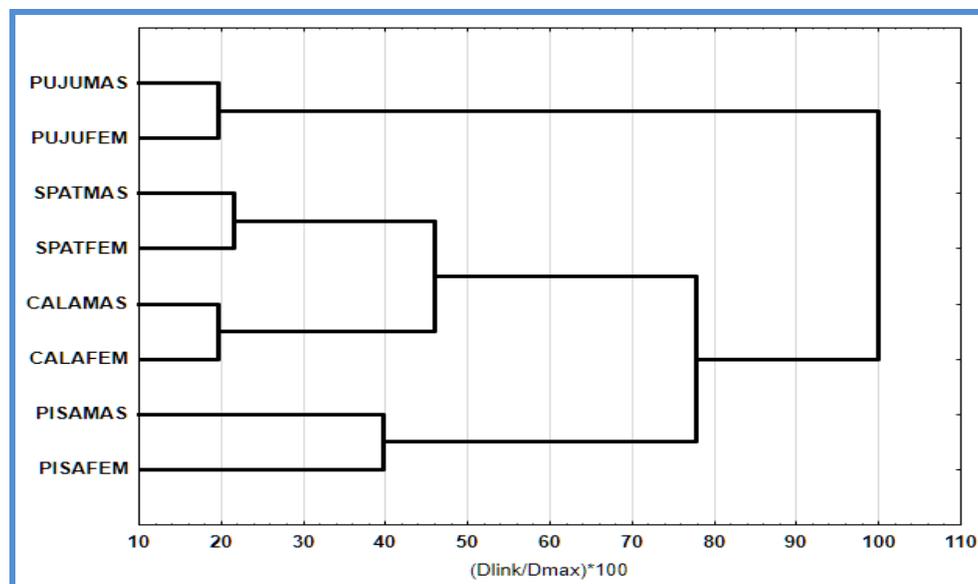


Figure 4: Sexual dimorphism by locality based on D^2 values Ward's method. Puna de Jujuy (PUJU), San Pedro de Atacama (SPAT), Calama (CALA) and Pisagua (PISA). The suffixes MAS and FEM are added as appropriate.

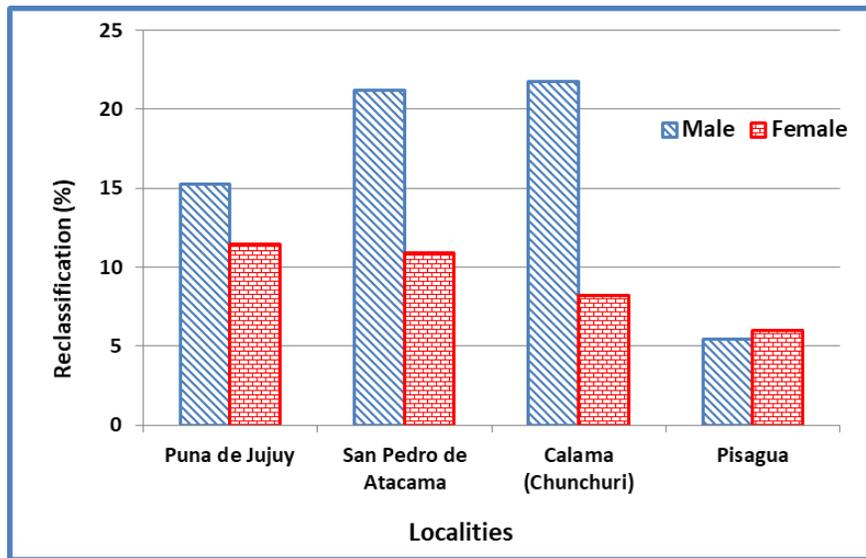


Figure 5: Reclassification of individuals by sex in a place other than the original one

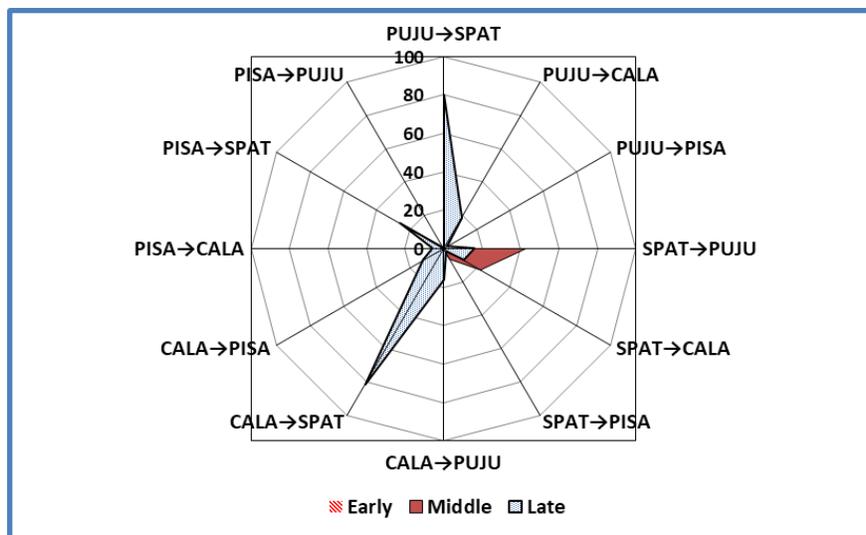


Figure 6: Reclassification (in %) of individuals by period in a place other than the original one

There is an inverse geographical correlation ($r=-0.88$, $p<0.05$) between the proportion of reclassified individuals and D^2 values among localities (Figure 7); SPAT and CALA are located at one extreme with the highest reclassification and the lowest D^2 value, and PUJU and PISA at the other extreme with the highest D^2 value and the lowest number of reclassified individuals. One outstanding fact is the correlation of the D^2 values between sexes: $r=0.85$ ($p<0.05$), from lower D^2 values among nearest localities such as CALA and SPAT to extreme values between PISA and PUJU (Figure 10).

Table 7: D² values. Differences between individuals of both sexes and between localities

Localities	Sex	Puna de Jujuy		San Pedro de Atacama		Calama (Chunchuri)		Pisagua	
		M	F	M	F	M	F	M	F
Puna de Jujuy	M	0.00	4.46	8.13	9.04	8.74	13.41	15.05	12.76
	F	4.46	0.00	12.90	7.42	12.83	12.88	22.70	14.35
San Pedro de Atacama	M	8.13	12.90	0.00	4.87	5.55	11.72	8.03	9.86
	F	9.04	7.42	4.87	0.00	6.83	6.05	15.68	8.09
Calama (Chunchuri)	M	8.74	12.83	5.55	6.83	0.00	4.46	10.69	10.03
	F	13.41	12.88	11.72	6.05	4.46	0.00	18.48	9.70
Pisagua	M	15.05	22.70	8.03	15.68	10.69	18.48	0.00	9.00
	F	12.76	14.35	9.86	8.09	10.03	9.70	9.00	0.00

Global difference: Wilks's Lambda: 0.092 approx. $F_{(203,7736)}=15.98$, $p<0.001$. Difference between pairs of comparisons (between sexes and between localities by sex), $p < 0.001$. M: Male, F: Female.

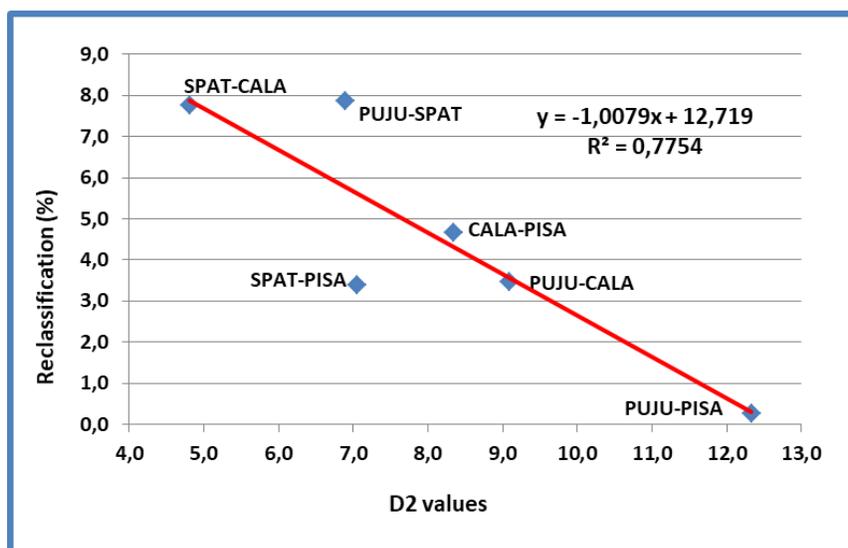


Figure 7: Correlation between D² values and the percentage of individuals reclassified in a site other than the original one ($r=-0.88$, $p<0.05$). PUJU: Puna de Jujuy, SPAT: San Pedro de Atacama, CALA: Calama (Chunchuri) and PISA: Pisagua.

Table 8: Fst values between localities and between localities by sex

Quitor (1)	N	Fst	se	
Total	326	0.0457	0.0115	
Males	166	0.0636	0.0198	Fst difference between sexes: 20%
Females	160	0.0765	0.0201	
PUJU-SPAT-CALA-PISA (2)	N	Fst	se	
Total	1168	0.0825	0.0030	
Sexes/Localities	1168	0.1193	0.0037	
Males/Localities	687	0.0919	0.0040	Fst difference between sexes: 18%
Females/Localities	481	0.1080	0.0059	

(1)Varela & Cocilovo, 2009; (2) This paper; PUJU (Puna de Jujuy), SPAT (San Pedro de Atacama), CALA (Calama), PISA (Pisagua); N: number of observations; se: standard error.

The structure of the regional population measured by the statistic $F_{st}=0.0825 \pm 0.0030$ indicates the magnitude of genetic divergence (Table 8). Figure 8 shows the expected pattern of equilibrium between drift and migration along the straight line and the distribution of localities by observed/expected variance. With the exception of PISA, which is in balance, the other localities have a different balance than expected.

The greater variance of PUJU indicates the composition of the gene pool from a greater geographic range. The lower variances observed in SPAT and CALA indicate a greater genetic interaction between nearby localities in the region itself. For this level of regional analysis, a global migration rate of 2.8 individuals per generation was estimated. According to the “stepping-stone” model, the average rate between neighboring localities is 0.036 per generation (Table 9) with the lowest value between PUJU and PISA (0.0116) and the highest between SPAT and CALA (0.1102).

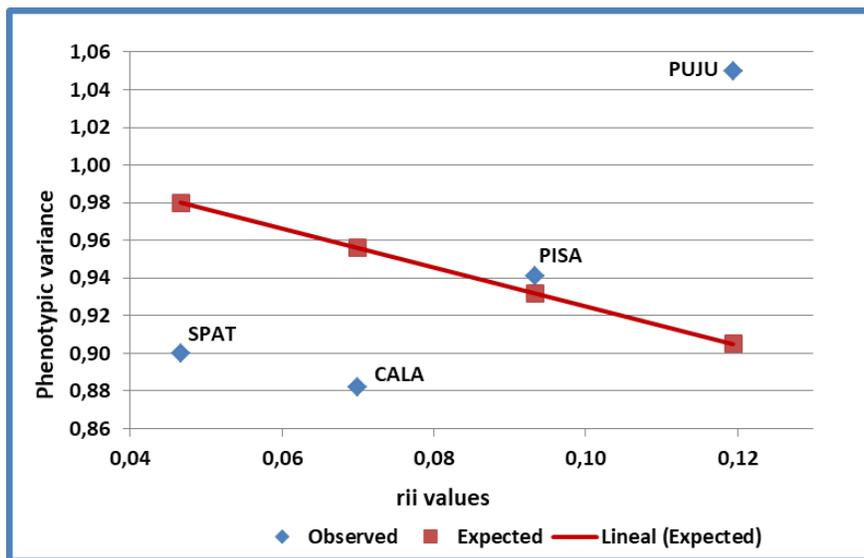


Figure 8: Observed and expected phenotypic variance for Puna de Jujuy (PUJU), San Pedro de Atacama (SPAT), Calama (CALA) and Pisagua (PISA). Values rii distance to the centroid of the distribution. F_{st} value = 0.0825 ± 0.0030

The properties of both sexes, although consistent with the previous result, reveal an increase of 45% in regional divergence ($F_{st}=0.1195\pm0.0037$). The greatest genetic variation is found in both PUJU sexes and in male PISA individuals (Figure 9). SPAT men and CALA individuals present a balance between effective size and migratory effect. In contrast, women in SPAT, CALA and PISA show a smaller variance than expected, due to their reduced effective size and the influence of increased local gene flow. A global migration rate of 1.8 individuals per generation was estimated. Migratory rates were calculated independently and between localities by sex, according to the “stepping-stone” model based on the Nm_m values for males and Nm_f for females. The results obtained reflect the variation in the number of migrants and the migration rate per generation according to the distance between localities, with male individuals' values predominating in relation to female individuals' (Table 9).

Table 9: Migration rates (M) between localities according the “stepping-stone” model (Slatkin 1994)

Distance between	km	M	Nm_m	M	Nm_f	M
PUJU SPAT	398	0.0280	3.98	0.0400	4.62	0.0465
PUJU CALA	498	0.0223	4.38	0.0352	2.60	0.0209
PUJU PISA	958	0.0116	1.94	0.0081	1.62	0.0068
SPAT CALA	101	0.1102	5.27	0.2085	3.96	0.1569
SPAT PISA	550	0.0202	4.28	0.0312	2.98	0.0217
CALA PISA	451	0.0247	2.99	0.0266	1.94	0.0172

PUJU (Puna de Jujuy), SPAT (San Pedro de Atacama), CALA (Calama) and PISA (Pisagua)

Figure 11 shows the distribution of F_{st} values among localities by sex from Table 10 with an acceptable correlation ($r=0.87$, $p<0.05$). In general, the effect of distance on the increase in this statistic from the lowest F_{st} value between SPAT and CALA to the highest F_{st} value between PUJU and PISA is also highlighted. Figure 12 analyses the migration rates between localities for each sex in comparison with the female sex (M_m-M_f)/ M_f . With the exception of PUJU-SPAT, where the feminine migratory effect predominates (13.9%), in the remaining comparisons and in the total estimate, the male migratory rate is higher.

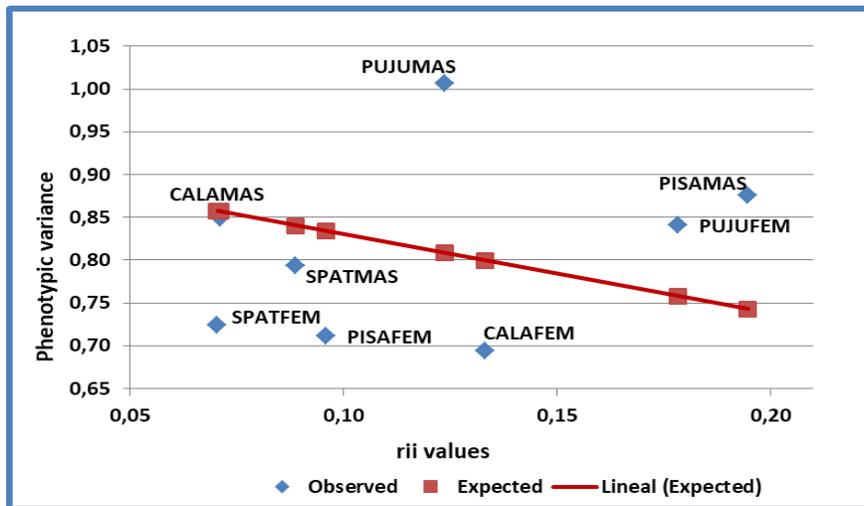


Figure 9: Observed and expected phenotypic variance for the male and female sexes of Puna de Jujuy (PUJU), San Pedro de Atacama (SPAT), Calama (CALA) and Pisagua (PISA). The suffixes MAS and FEM are added as appropriate. Values rii distance to the centroid of the distribution. Fst value = 0.1195 ± 0.0037.

Table 10: Fst values and standard error (se) between sexes and localities

Localities	Sex	Puna de Jujuy	San Pedro de Atacama	Calama (Chunchuri)	Pisagua
Puna de Jujuy	M	0.0270	0.0591 (±0.0026)	0.0540 (±0.0033)	0.1141 (±0.0069)
	F	(±0.0026)	0.0513 (±0.0031)	0.0876 (±0.0062)	0.1337 (±0.0099)
San Pedro de Atacama	M		0.0398	0.0453 (±0.0029)	0.0551 (±0.0053)
	F		(±0.00200)	0.0594 (±0.0049)	0.0774 (±0.0081)
Calama (Chunchuri)	M			0.0303	0.0770 (±0.0065)
	F			(±0.0042)	0.1141 (±0.0106)
Pisagua	M				0.0815
	F				(±0.0102)

M: males, F: females

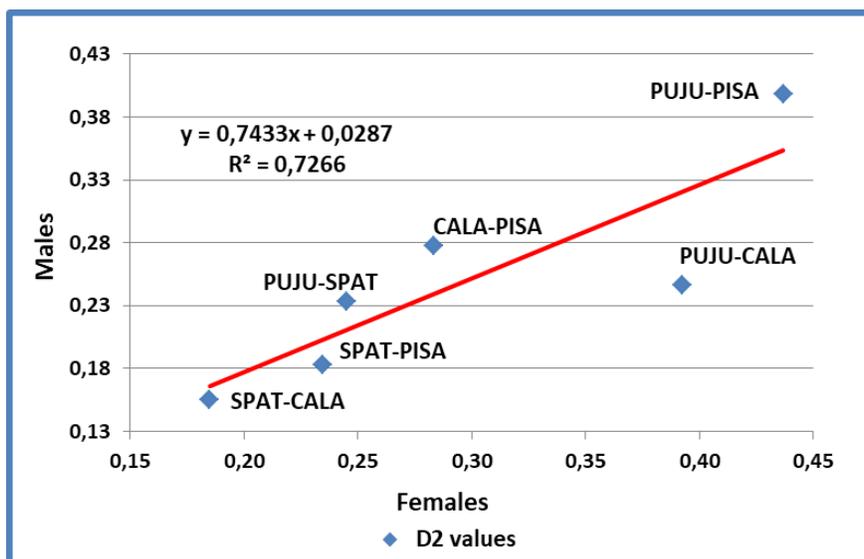


Figure 10: Correlation between D^2_m (male) and D^2_f (female) values ($r=0.85$, $p<0.05$). PUJU: Puna de Jujuy, SPAT: San Pedro de Atacama, CALA: Calama (Chunchuri) and PISA: Pisagua. M: Male, F: Female.

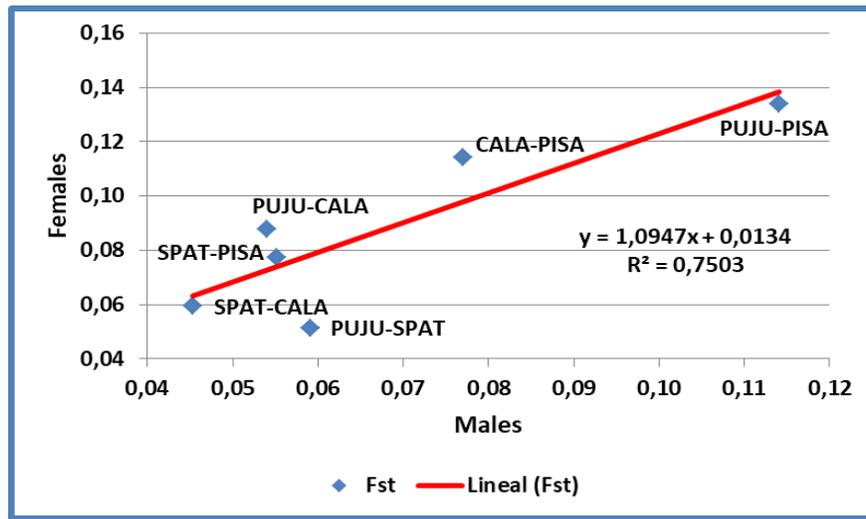


Figure 11: Fst values between locations for each sex ($r=0.87$, $p<0.05$). PUJU: Puna de Jujuy, SPAT: San Pedro de Atacama, CALA: Calama (Chunchuri) and PISA: Pisagua.

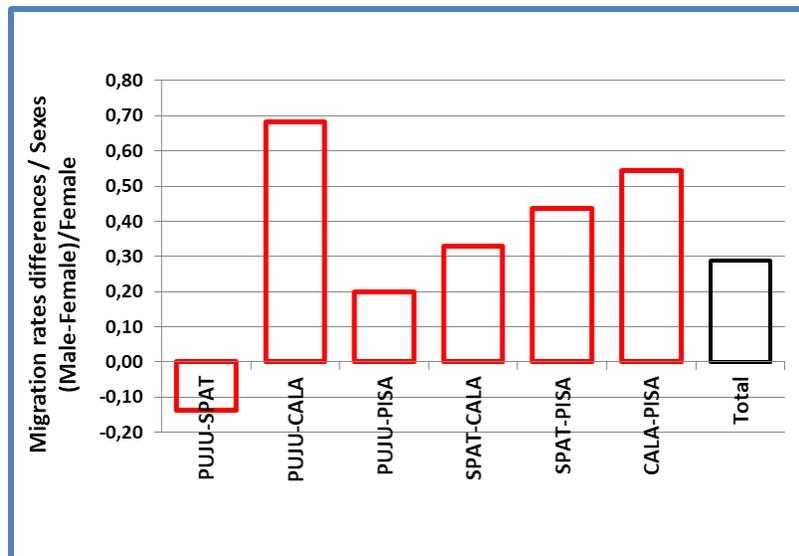


Figure 12: Male-female migration rates between sites. PUJU: Puna de Jujuy, SPAT: San Pedro de Atacama, CALA: Calama (Chunchuri) and PISA: Pisagua.

4. Discussion

The distribution of the sexes among localities (Table 2) suggests the existence of different residential patterns and work habits. In the total sample, the number of men exceeds the number of women by 43%, possibly due to their relationship with regional traffic. The analysis of artificial deformation indicates the particular integration of local societies in which members of different origins coexist, with different customs, traditions and cultural patterns. The individuals without deformation (33%) are distributed in similar proportions in the different localities. In general, in the route between PUJU and PISA, tabular shapes predominate with a frequency six times greater than circular shapes, which are distributed on the same route with increasing frequencies from east to west (Table 3). It has been found that i) in the NCH the frequency of circular shapes is much higher than in the NOA (23% and 2% respectively), the same as the cases without deformation (28% and 11%) and ii) in the NOA the tabular forms are predominant compared to the NCH (86% and 50%) (Cocilovo & Varela, 2010). The phenotypic differences among localities (Figure 2 and Table 4) confirm results from previous partial researches (Cocilovo et al., 2017; Fuchs et al., 2016b) and allow for a wider understanding of the relationships between the societies distributed along the route from the PUJU to the Pacific coast of the NCH.

The impact of the migratory effect on genetic divergence and stability of local phenotypes is important. The effect of distance influenced the properties revealed by the different statistics employed in this study. The D^2 values between localities clearly reflect the spatial effect (Figure 3) with a significant direct correlation value ($r=0.94$, $p<0.05$). This effect is also manifest in the information in tables 5 and 6, which highlight the extinction of the probability of classifying individuals in a different group according to the geographical distance separating the origin sites. Besides, it is also observed in the inverse relationship between D^2 values and the proportion of reclassified individuals (Figure 7).

These facts are related to the linear decrease in kinship between PUJU and PISA according to the distance isolation model (Cocilovo & Rothhammer, 1999; Morton, 1977, 1982) and the increase in the differences of each sex according to the distance between localities (Table 7). The proportion of individuals reclassified into a different group by chronological period; dominating the frequency in the Late Period, lower in the Middle Period and very low in the Early Period (Figure 6), is related to the growth of local populations and the increase in relationships on the route between PUJU and PISA. The efficiency of the reclassification analysis was also confirmed in earlier work by testing the relationship of SPAT individuals assigned to the group itself with significant probabilities associated with relevant contextual materials and with $^{87}\text{Sr}/^{86}\text{Sr}$ isotope tags for SPAT (Cocilovo et al., 2017).

The observed variance in PUJU (Figure 8) explains the integration of a genetic variability of a wider range (greater heterozygosis) compared to the other localities including men and women. The integration of the PUJU population is related to Cochabamba in southern Bolivia and the Quebrada de Humahuaca in the NOA. Such an association is derived from the results of the study of several CSAA locations (Varela et al., 2008, ms). While in PISA a balance is noted between the observed and expected variances, SPAT and CALA are related to a more restricted geographical circuit. This effect is determined by the genetic composition of women (higher homozygosis) of SPAT, CALA and PISA as seen in Figure 9. These results reflect the general migration rates in both experiences of 2.8 and 1.8 individuals per generation respectively, in the first case by the effect of PUJU and in the second case because of lower variability in the women of SPAT, CALA and PISA. In fact, if an analogy could be established, the sex less reclassified in a group other than the original group is female (36%) compared to male (64%) (Figure 5). The position of PISA men in Figure 9 is produced by the contribution of genetic variability from a greater territorial area of the NCH, both on the coast and inland, whose antecedents date back to the Archaic Period, linking the coast with the interior valleys (Standen & Núñez, 1984).

The composition of the Pisagua human group reflects the relationship with a wide range of population events in the intermediate basins of the NCH linked to the San Pedro de Atacama Salar, Pampa del Tamarugal and Quebrada de Tarapacá (Cocilovo, 1994). From evidence of textiles, the study carried out by Agüero (1995, 2009) proved the integration of Pisagua within a wide territory from Camarones and the Quebrada de Tarapacá in the Formative Period (890 BC - 290 AD) and in the Late Intermediate Period with the Pica-Tarapacá Complex covering a broader area of interaction of the NCH and the south of Peru. This interaction continued until the Late and Inca Period in the "Triple Frontier" environment (southern Peru and Bolivia, NOA and NCH) by the caravan practices based on kinship, the exchange of products, knowledge and ideologies and commercial relations (Nielsen, 2013).

The evidence obtained indicates a much more complex population structure than expected by the different properties of both sexes in terms of local and regional genetic variation. Although there is an acceptable correlation of D^2 values between male and female (Figure 10), the cases of CALA-PISA, PISA-PUJU and CALA-PUJU indicate variations in local dimorphism perhaps due to the integration of populations with individuals of different origins, which is highlighted by the greater sexual dimorphism in PISA compared to other localities (Figure 4). This effect could also be related to a differential migratory circuit between localities and is illustrated in the analysis of migratory rates by the stepping-stone model (Table 9) and in the relationship between the estimated migratory rates between both sexes in which males predominate (Figure 12).

The results gained suggest an important research topic related to residential patterns of both sexes (patrilocal/matrilocal), preferential marriages, marriage alliances, etc. This paper provides a first approximation (Table 8) including results obtained previously in the analysis of the SPAT Quito site by cultural periods (Early, Middle and Late) in which the differences between the F_{st} feminine value was verified, exceeding by 20% (0.0765 ± 0.0201) the F_{st} masculine value (0.0636 ± 0.0198) (Varela & Cocilovo, 2009). A similar difference was found in the present study in which the F_{st} value among localities of the female component was 18% higher than the estimated F_{st} value for the male component. The difference is due to the greater heterogeneity of women between localities due to a greater local genetic input or smaller effective size. This event may be the result of a model of post marital matrilineal residence.

The graph in Figure 10 is quite illustrative with respect to the trans-Andean localities when comparing the D^2 values between localities obtained for both sexes, since the D^2 values for males are generally lower than for females. The analysis of the correlation of F_{st} values between sexes (Figure 11) indicates the cases (except for PUJU-SPAT) in which women have higher value than men (CALA-PISA, SPAT-PISA, PUJU-CALA, SPAT-CALA), revealing a particular sex-specific structure (Table 10) with greater diversity, smaller effective size and less migratory effect. These results are consistent with the residential relationships expected according to Konigsberg (1988) and Konigsberg and Frankenberg (2016): if a sex has greater mobility within a migration circuit and a higher migration rate, its genetic variance between groups will be lower and there will be a greater variance within the group with respect to the less mobile sex in the current generation. Differences in effective size between the sexes can be explained by variation in reproductive success (polygyny), progeny rules, and transmission of reproductive success (Heyer et al., 2012).

The highlighted events may relate to population movements or mostly male migrations associated with trafficking and product exchange through llama caravans. However, it is interesting to consider in the Atacamenian area the possible survival of ancestral customs that are projected in the Hispanic-Indigenous Period with migrations mainly due to the work of men and unmarried women with children. In addition, the survival of ancient customs of extramarital relations perhaps was favored by the limited number of men in each *ayllu*, situation that in pre-Hispanic times may not have been different given the high mobility of these peoples who were often shepherds and traffickers (Difrieri, 1980). The current study found that 84% of the individuals reclassified in a different locality were of adult and mature ages, mostly male (Figure 5).

The genetic variation determined is the product of an ancient evolutionary process that dominated a vast region of the Central-South Andean Area whose avatars shaped the genetic profile of the populations at a local and regional level. This process explains the magnitude of the estimated F_{st} values among localities and between the sexes (Tables 8 and 10). In later moments of regional history, population growth and increased interaction between different localities determined the relationship of variances within and between groups. This ratio reached similar values indicated by a F_{st} of 2.6% in the final period of the SPAT developments (Varela & Cocilovo, 2011), 2.5% of PUJU (Fuchs et al., 2016a) and the overall value determined between PUJU and SPAT of 2.4% (Cocilovo et al., 2017). In the Late Final Period the migration rate (Nm) between these localities could have reached an average of 10 individuals per generation, marking the highest level of regional interaction.

The results obtained here are consistent with estimates made in previous studies. At the regional level, between Southern Bolivia, NOA and NCH, the statistic $F_{st}=0.0976\pm 0.0036$ (Varela et al., 2008) reflects the genetic variability of a wide region and underpins the diversity generated from the initial population with an average migration rate of 2.3 individuals per generation. This variability manifests itself in localities with F_{st} values revealing the map of regional genetic history. For example, in Quitor *Ayllu* (SPAT), the total F_{st} value was estimated to be 0.0457 ± 0.0115 between different chronological periods (Varela & Cocilovo, 2009), very close to the value $F_{st}=0.0481 \pm 0.0068$ integrating most of the SPAT sites and periods (Varela & Cocilovo, 2011). The statistics obtained for the route between PUJU and PISA on the Pacific coast reveals an increase in genetic divergence from 8% between localities to 12% between localities for both sexes over a distance greater than approximately 1000 km. The migration rate was between 2.8 and 1.8 individuals/generation, an average of 0.036 taking into account the distances between localities.

In summary, 1) Geographical factor was the main factor in the modelling of population structure and population dynamics. Genetic divergence is proportional to the distance between localities. There were statistically significant differences between mean phenotypes of PUJU, SPAT, CALA and PISA (D^2 and Wilks' Lambda) localities, between phenotypes of both sexes in each locality and in the correlation between D^2 values and distances between localities.

2) In the total sample, 16% of the individuals were reclassified in a different group from the original one, with greater frequency of men. The majority of individuals were of adult and mature ages. Frequencies and probabilities of assignment to a different group gradually decrease with distance. The effect of distance determines the significant inverse correlation between the proportion of reclassified individuals and D^2 values.

3) In general, there are few individuals reassigned to the Early Period and individuals are predominantly classified in the Middle and Late periods during which the greatest regional interaction occurs.

4) The analysis of population structure established that local migration processes had more influence on the genetic composition of females and regional migration processes had more influence on the genetic composition of males.

Fst values among localities for both sexes indicate an increase of 45% of the divergence, with higher values in females ($F_{st}=0.1084 \pm 0.0059$) and lower values in males ($F_{st}=0.0919 \pm 0.0040$). The correlation between Fst values of each sex and the highest male migration rate compared to female migration is emphasized. The tests conducted indicate the stability of mean phenotypes in each locality and the random distribution of environmental effects.

5) This paper highlights the reliability of the evidence that supports the main factors that determine the evolution of populations. The reconstruction of the evolutionary process from the origin of the territorial settlement requires more information only possible from the recovery and responsible conservation of ancient human remains obtained during the excavations of archaeological sites.

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