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 Fst statistic was calculated to determine the genetic structure and the kinship relationships within and between populations. The Fst value between localities is Fst=0.0825 ± 0.0030. Considering the sexes by site, the observed genotypic variance (Fst=0.1195 ± 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 matrilocal 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 ⁸⁷Sr/⁸⁶Sr 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).
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, Sorcuy and Tablada de Abra Pampa) with dates in the interval of 964 ± 45 AP (cal d.C 1029-1208 ± 2σ) for the Pucará de Rinconada and 501 ± 42 AP (cal d.C 1400-1497± 2σ) 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 sex, of 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 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.

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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.

| Metric variable                  | Definition                                          |
|---------------------------------|-----------------------------------------------------|
| Maximum cranial length          | Basion-prosthion length                             |
| Maximum cranial breadth         | Nasion-prosthion height                             |
| Basion-bregma height            | Nasal height                                        |
| Porion-bregma height            | Nasal breadth                                       |
| Minimum frontal breadth         | Cheek height                                        |
| Maximum frontal breadth         | Biobital breadth                                    |
| Upper facial breadth            | Orbital breadth left                                |
| Bizygomatic breadth             | Orbital height left                                 |
| Bimaxillary breadth             | Maxillo-alveolar breadth                            |
| Basion-nasion length            | Maxillo-alveolar length                             |

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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 Fst 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 Fst 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, Fst 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 ($G = h^2 F$). 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 Fst 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 Fst 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 Fst 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: $N_m=1/4 *[1/(1/Fst)-1]$. 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 $M=4N_m/k$, 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          |       |       |       |
|---------------------|--------------|-------|-------|-------|
|                     | Male         | Female| Total |       |
| 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 |
| 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 \( D^2 \) 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                |        |
|                     | p       | 0.11          | 0.03                 | 0.01               |        |
| San Pedro de Atacama| %       | 5.8           | 3.4                  | 1.0                |        |
|                     | p       | 0.06          | 0.06                 | 0.02               |        |
| Calama (Chunchuri)  | %       | 5.0           | 24.8                 | 3.7                |        |
|                     | p       | 0.05          | 0.18                 | 0.02               |        |
| Pisagua             | %       | 0.0           | 31.5                 | 7.4                |        |
|                     | p       | 0.03          | 0.13                 | 0.05               |        |

Total of reclassified individuals: 187 (16%)

Table 7 shows the analysis of the sex differences based on D² 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 D² (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 D² 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.
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: $D^2$ values. Differences between individuals of both sexes and between localities

| Localities         | Sex | Puna de Jujuy | San Pedro de Atacama | Calama (Chunchuri) | Pisagua |
|--------------------|-----|---------------|----------------------|--------------------|--------|
|                    | M   | M             | M                    | M                  | M      |
| Puna de Jujuy      |     | 0.00          | 4.46                 | 8.13               | 9.04   |
|                    | F   | 4.46          | 0.00                 | 12.90              | 7.42   |
| San Pedro de Atacama | M  | 8.13          | 12.90                | 0.00               | 4.87   |
|                    | F   | 9.04          | 7.42                 | 4.87               | 0.00   |
| Calama (Chunchuri) | M   | 8.74          | 12.83                | 5.55               | 6.83   |
|                    | F   | 15.05         | 22.70                | 8.03               | 9.86   |
| Pisagua            | M   | 15.05         | 22.70                | 8.03               | 9.86   |
|                    | F   | 12.76         | 14.35                | 9.86               | 9.00   |

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 $D^2$ 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 |
| Females          | 160 | 0.0765 | 0.0201 |

Fst difference between sexes: 20%

| 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 |
| Females/Localities      | 481 | 0.1080 | 0.0059 |

Fst difference between sexes: 18%

(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 $Fst=0.0825 \pm 0.0030$ 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).

![Image of observed and expected phenotypic variance](image)

**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. Fst value = 0.0825 ± 0.0030

The properties of both sexes, although consistent with the previous result, reveal an increase of 45% in regional divergence (Fst=0.1195±0.0037). 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 values for males and Nm 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).

| 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 Fst 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 Fst value between SPAT and CALA to the highest Fst 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 (Mm-Mf)/Mf. 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 (±0.0026) | 0.0591 (±0.0026) | 0.0540 (±0.0033) | 0.1141 (±0.0069) |
|                     | F   |               | 0.0513 (±0.0031) | 0.0876 (±0.0062) | 0.1337 (±0.0099) |
| San Pedro de Atacama| M   |               | 0.0398 (±0.00200) | 0.0453 (±0.0029) | 0.0551 (±0.0053) |
|                     | F   |               |                       | 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 $D_{2m}$ (male) and $D_{2f}$ (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.
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 Quitor site by cultural periods (Early, Middle and Late) in which the differences between the Fst feminine value was verified, exceeding by 20% ($0.0765 \pm 0.0201$) the Fst masculine value ($0.0636 \pm 0.0198$) (Varela & Cocilovo, 2009). A similar difference was found in the present study in which the Fst value among localities of the female component was 18% higher than the estimated Fst 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 matrilocal 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 Fst values between sexes (Figure 11) indicates the cases (except for PUJU–SPAT) in which women have higher values 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 Atacamian 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 aillu, 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 Fst 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 Fst 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 \( Fst=0.0976 \pm 0.0036 \) (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 Fst values revealing the map of regional genetic history. For example, in Quitor Ayllu (SPAT), the total Fst value was estimated to be 0.0457 ± 0.0115 between different chronological periods (Varela & Cocilovo, 2009), very close to the value \( Fst=0.0481 \pm 0.0068 \) 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 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 (Fst=0.1084 ± 0.0059) and lower values in males (Fst=0.0919 ± 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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5. References

Agüero, C., (1995). El Cementerio “D” Protonazca de Pisagua. Análisis de la Textilería, Hombre y Desierto Una Perspectiva Cultural, Actas XIII Congreso Nacional de Arqueología Chilena, Tomo II, Comunicaciones 9, 7-16, Sociedad Chilena de Arqueología, Antofagasta.

Agüero, C., (2009). La Colección “Tiahuanaco” de Uhle y su relación con el Complejo Pica Tarapacá (norte de Chile): Actas IV Jornadas Internacionales sobre Textiles Precolombinos, 439-458, Universidad Autónoma de Barcelon.

Bass, W. M., (1981). Human Osteology: A laboratory and field manual of the human skeleton, University of Missouri Press, Springfield.

Betti, L., Balloux, F., Hanihara, T., & Manica, A., (2010). The Relative Role of Drift and Selection in Shaping the Human Skull, American Journal of Physical Anthropology 141, 76-82.

Buikstra, J. E., & Ubelaker, D., (1994). Standards for data collection from human skeletal remains. Research series no. 44. Fayetteville, Arkansas: Arkansas archeological survey research series nº 44.

Cocilovo, J. A., (1994). Biología de la población prehistórica de Pisagua. Continuidad y cambio biocultural en el Norte de Chile. Tesis Carrera de Doctorado en Ciencias Biológicas, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de Córdoba.

Cocilovo, J. A., & Rothhammer, F., (1999). Microevolución morfológica y extinción del parentesco en asentamientos humanos prehistóricos del Valle de Azapa, Chile. Revista Chilena de Historia Natural, 72, 213-218.

Cocilovo, J. A., & Varela, H. H., (1999). Variación Morfológica, Estructura Canónica y Bioensayo de Parentesco en Poblaciones Prehistóricas del Norte de Chile. Chungara, 30 (1),75-85.

Cocilovo, J. A., & Varela, H. H., (2010). La distribución de la deformación artificial del cráneo en el Área Andina Centro Sur. Relaciones de la Sociedad Argentina de Antropología 35, 41-68.

Cocilovo, J. A., Varela, H. H., & Fuchs, M. L., (2017). Divergencia fenotípica y flujo génico en el Área Andina Centro Sur: el trayecto entre Puna de Jujuy, San Pedro de Atacama y Calama. Antropo, 37, 1-15, www.didac.ehu.es/antropo/37/37-01/Cocilovo.pdf

Cocilovo, J. A., Varela, H. H., & O’Brien, T. G., (2009). La divergencia genética entre poblaciones del Área Andina Centro Meridional evaluada mediante rasgos no métricos del cráneo. Revista Argentina de Antropología Biológica, 11(1), 43-59.

Cocilovo, J. A., Varela, H. H., & Valdano, S. G., (2016). La Población Prehistórica de Calama Chunchurí Norte de Chile. Composición y Estructura. Boletín del Museo Nacional de Historia Natural, Chile, 65, 291-306.

Cocilovo, J. A., Varela, H. H., Fuchs, M. L., & Valdano, S. G., (2017). Movilidad, Tráfico Sur Andino y Diferenciación Genética entre San Pedro de Atacama y la Puna de Jujuy. Relaciones de la Sociedad Argentina de Antropología, 42 (2), 207-229.
Cocilovo, J. A., Quevedo, S., Varela, H. H., Valdano, S. G., & Castro, M., (1999). Biología del grupo prehistórico de Pisagua costa norte de Chile. Estudios Atacameños, 17, 207-235.

Convención Internacional de Mónaco 1906. In Comas, J. 1966 Manual de Antropología Física, Apéndice 1, Universidad Autónoma de México.

Costa, M. A., & Llagostera, A., (2014). Leishmaniasis en Coyo Oriente. Migrantes trasandinos en San Pedro de Atacama, Estudios Atacameños Arqueología y Antropología Surandinas 47, 5-18.

Costa, M. A., Matheson, C., Iachetta, L., Llagostera, A., & Appenzeller, O., (2009). Ancient Leishmaniasis in a Highland Desert of Northern Chile, PLoS ONE, 4(9) e6983. doi.org/10.1371/journal.pone.0006983.

De Nigris, M. R., (2009) Arqueología Minería y Metalurgia en la localidad de Cobres y sus alrededores Periodos Prehispánicos y Colonial, Universidad Nacional de Salta.

Dembo, A., & Imbelloni, J., (1938). Deformaciones intencionales del cuerpo humano. Humanior, Sección A 3. Buenos Aires, Imprenta Luis L. Gotelli.

Difrieri, H., (1980). La Población de Atacama en el Siglo XVII. Boletín del Instituto de Historia Argentina y Americana “Dr. E. Ravignani”, 16 (26), 163-203.

Durán, E., Kangiser, M. F., & Acevedo, N., (2000). Colección Max Uhle: Expedición a Calama 1912. Publicación Ocasional del Museo Nacional de Historia Natural (Chile), 56, 5-49.

Falconer, D. S., & Mackay, T. F. C., (1996). Introduction to Quantitative Genetics, 4º Ed. Logman.

Fuchs, M. L., (2014). Caracterización bioestructural de la población antigua de la Puna de Jujuy (Argentina). Tesis doctoral inédita, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, Universidad Nacional de Río Cuarto, Argentina.

Fuchs, M. L., & Varela, H. H., (2013). Fechados radiocarbónicos de Colecciones osteológicas de la Puna de Jujuy, Argentina. Relaciones de la Sociedad Argentina de Antropología, 38, 553-558.

Fuchs, M. L., Varela, H. H., & Cocilovo, J. A., (2016a). Kinship and Phenotypic Divergence in the Ancient Population of the Puna Plateau of Northwestern Argentina. Advances in Anthropology, 6, 1-10.

Fuchs, M. L., Varela, H. H., & Cocilovo, J. A., (2016b). Relaciones biológicas entre la Puna de Jujuy Argentina y San Pedro de Atacama Chile. Antropo 36, 15-27.

Genovés, S., (1962). Introducción al Diagnóstico de la Edad y del Sexo en Restos Óseos Prehistóricos. Publicación del Instituto de Historia, México.

Grosjean, M., Núñez, L., & Cartajena, I., (2005). Paleoindian occupation in the Atacama Desert, Northern Chile. Journal of Quaternary Science, 20, 643-653.

Heyer, E., Chaix, R., Pavard, S., & Austerlitz, F., (2012). Sex-specific demographic behaviors that shape human genomic variation. Molecular Ecology, 21, 597-612.

Knudson, K. J., Pestle, W. J., Torres-Rouff, C., & Pimentel, G., (2012). Assessing the life history of an andean traveller through biogeochemistry: Stable and radiogenic isotope analyses of archaeological human remains from Northern Chile. International Journal of Osteoarchaeology, 22, 435-451.

Konigsberg, L. W., (1988). Migration Models of Prehistoric Postmarital Residence. American Journal of Physical Anthropology, 77, 471-482.

Konigsberg, L. W., & Frankenber, S. R., (2016). Postmarital residence analysis. In Biological Distance Analysis: Forensic and Bioarchaeological Perspectives (pp. 335-347). Elsevier Inc. DOI: 10.1016/B978-0-12-801966-5.00018-4

Konigsberg, L. W., & Ousley, S. D., (1995). Multivariate quantitative genetics of anthropometric traits from the Boas data. Human Biology, 81(5-6), 579-594.

Latorre, C., Santoro, C. M., Ugalde, P. C., Gayo, E. M., Osorio, D., Salas-Egaña, C., De Pol-Holz, R., Joly, D., & Rech, J. A., (2013). Late Pleistocene human occupation of the hyperarid core in the Atacama Desert, northern Chile. Quaternary Science Reviews, 77 (2013) 19e30.

Lecoq, P., (1987). Caravanes de lamas, sel et échanges dans une communauté de Potosi, en Bolivie, Bulletin de l'Institut français d'études andines, 16 (2-4), 1-38.

Llagostera, A., (1995). El componente Aguada en San Pedro de Atacama. Boletín del Museo Chileno de Arte Precolombino, 6, 9-34.

Llagostera, A., Torres, C. M., & Costa, M. A., (1988). Complejo psicotrópico de Solcor-3 (San Pedro de Atacama). Estudios Atacameños, 9, 61-98.

Medeot, E. A., Cocilovo, J. A., & Varela, H. H., (2008). Varianza ambiental y estabilidad del desarrollo en la Población prehispánica de Las Pírquas (Salta, Argentina), Latin American Antiquity, 19(2), 146-157.
Molina Otárola, R., (2011). Los otros arrieros de los valles La Puna y el Desierto de Atacama. Chungara Revista de Antropología Chilena, 43 (2), 177-187.
Montenegro, M., & Ruiz, M., (2007). Tránsito y Paisaje en la Puna de Jujuy durante los Desarrollos Regionales: Una Aproximación Iconográfica. Cuadernos FHyCS-UNJu, 32, 167-185.
Montes Suay, F., (2007). Introducción a la Probabilidad, Departamento de Estadística e Investigación Operativa, Universitat de València, España.
Morton, N. E., (1977). Isolation by distance in human population. Annals of Human Genetics, 40, 361-365.
Morton, N. E., (1982). Outline of Genetic Epidemiology, S. Karger, New York.
Nielsen, A. E., (1997-1998). Tráfico de Caravanas en el sur de Bolivia: Observaciones etnográficas e implicancias arqueológicas. Relaciones de la Sociedad Argentina de Antropología, 22-23, 139-178.
Nielsen, A. E., (2002). Asentamientos, conflicto y cambio social en el altiplano de Lípez (Potosí). Revista Española de Antropología Americana, 32, 179-205.
Nielsen, A. E., (2011). El Tráfico de Caravanas entre Lípez y Atacama visto desde la Cordillera Occidental. In L. Núñez, & A. E. Nielsen (Eds.), Ruta Arqueología Historia y Etnografía del Tráfico Sur Andino (pp. 83-110).
Nielsen, A. E., (2013). Circulating Objects and the Constitution of South Andean Society (500 BC - AD 1550). In K. G. Hirth & Pillsbury, J (Eds.), Merchants, Markets, and Exchange in the Pre-Columbian World (pp. 389-418), Dumbarton Oaks Research Library and Collection, Washington, D.C.
Núñez, L., (1965). Desarrollo Cultural Prehispánico del Norte de Chile. Estudios Antropológicos, 1, 37-115.
Núñez, L., (1968). Subárea Loa-Costa Chilena desde Copiapó a Pisagua. In Actas 32 Congreso Internacional de Americanistas, 145-182.
Núñez, L., (1976). Registro regional de fechas radiocarbónicas en el Norte de Chile. Estudios Atacameños, 4, 74-123.
Núñez, L., (1980). Cazadores tempranos en los Andes Meridionales. Evaluación cronológica de las industrias líticas del norte de Chile. Boletín de Antropología Americana, 2, 87-120.
Núñez, L., & Dillehay, T., (1995). Movilidad giratoria armonía social y desarrollo en los Andes Meridionales: Patrones de tráfico e interacción económica. (2nd ed.), Antofagasta: Universidad Católica del Norte.
Núñez, L., & Moraga, C., (1978). Ocupación arcaica temprana en Tiliviche, Norte de Chile (I región). Boletín del Museo Arqueológico de la Serena, 16, 45-59.
Núñez, L., & Pimentel, G., (2008). Informe prospección arqueológica proyecto exploración geológica de óxidos y sulfuros, División Codelco Norte, Chile.
Núñez, L., Grosjean, M., & Cartajena, I., (2002). Human occupations and climate change in the Puna de Atacama, Chile. Science, 298, 821-824.
Núñez, L., & Cartajena, I., (2010). Sequential Analysis of Human Occupation Patterns and Resource use In the Atacama Desert. Chungara, Revista de Antropología Chilena 42(2), 363-391.
Quevedo, S., & Cocilovo, J. A., (1994). El cementerio Protonazca de Pisagua (“D” Colección Max Uhle 1913). Caracterización Biocultural, Hombre y Desierto Una Perspectiva Cultural, Actas XIII Congreso Nacional de Arqueología Chilena, Tomo II, Comunicaciones 9, Sociedad Chilena de Arqueología, Antofagasta.
Quevedo, S., & Cocilovo, J. A., (1995). La Población Antigua de Pisagua. Caracterización Bioantropológica del Cementerio “C” de la colección Max Uhle, Informes DIBAM 4:46-53, Ciencias Sociales, Proyecto 95-15, 46-55, Santiago, Chile.
Relethford, J. H., (1994). Cranio metric variance among modern human populations. American Journal of Physical Anthropology, 95, 53-62.
Relethford, J. H., (1996). Genetic drift can obscure population history: problem and solution. Human Biology, 68, 29-44.
Relethford, J. H., (2001). Global analysis of regional differences in cranio metric diversity and population substructure. Human Biology, 73, 629-636.
Relethford, J. H., (2002). Apportionment of Global Human Genetic Diversity Based on Cranio metrics and Skin Color. American Journal of Physical Anthropology, 118, 393-398.
Relethford, J. H., & Blangero, J., (1990). Detection of differential gene flow patterns of quantitative variation. Human Biology, 62, 5-25.
Relethford, J. H., Harpending, H. C., (1994). Cranio metric variation, genetic theory, and modern human origins. American Journal of Physical Anthropology, 95, 249-270.
Relethford, J. H., Crawford, M. H., & Blangero, J., (1997). Genetic drift and gene flow in post-famine Ireland. Human Biology, 69, 443-465.

Seber, G. A. F., (1984). Multivariate observation, New York: John Wiley & Sons.

Slatkin, M., (1994). Gene flow and population structure. In L. Real (Ed.) Ecological Genetics, Princeton.

Sparks, C. S., & Jantz, R. L., (2002). A reassessment of human cranial plasticity: Boas revisited, Proceedings of the National Academy of Sciences, 99(23), 14636-14639, www.pnas.org/cgi/doi/10.1073/pnas.222389599

Standen, R. V., & Núñez, L., (1984). Indicadores antropológico-físico y culturales del cementerio precerámico Tiliviche-2 (Norte de Chile), Revista Chungara, 12,135-154.

Tarragó, M., (1977). Relaciones prehispánicas entre San Pedro de Atacama Norte de Chile y regiones aledañas: la Quebrada de Humahuaca, Estudios Atacameños, 5, 50-63.

Tarragó, M., (1984). La historia de los pueblos circumpuneños en relación con el altiplano y los Andes Meridionales. Estudios Atacameños, 7, 93-104.

Tarragó, M., (1989). Contribución al conocimiento arqueológico de las poblaciones de los oasis de San Pedro de Atacama en relación con los otros pueblos punoños, en especial, el sector septentrional del valle Calchaquí. Tesis para optar el título de Doctor en Historia, Especialidad Antropología, Universidad Nacional de Rosario.

Torres-Rouff, C., Knudson, K. J., Pestle, W. J., & Stovel, E. M., (2015). Tiwanaku Influence and Social Inequality: A Bioarchaeological, Biogeochemical, and Contextual Analysis of the Larache Cemetery, San Pedro de Atacama, Northern Chile. American Journal of Physical Anthropology, 158, 592-606.

Varela, H. H., & Cocilovo, J. A. (1999). Evaluation of the environmental component of the phenotypic variance in prehistoric population. Homo, 50, 46-53.

Varela, H. H., & Cocilovo, J. A., (2000). Structure of the prehistoric population of San Pedro de Atacama. Current Anthropology, 41, 125-131.

Varela, H. H. & Cocilovo, J.A., (2007). Phenotypic, Maximum Genetic, and Special Environmental Variability in Prehistoric Human Populations. American Journal of Physical Anthropology, 132, 17-24.

Varela H.H. & Cocilovo, J.A. & O'Brien, T.G., (2013). Valley to Valley: The Biological Connection between Prehispanic Residents of Cochabamba Bolivia and Azapa Chile. Advances in Anthropology, 34, 210-215, Published Online November 2013 in SciRes, http://dx.doi.org/10.4236/aa.2013.34030.

Varela H. H., O'Brien T. G. & Cocilovo J. A., (2008). The genetic divergence of prehistoric populations of the South-Central Andes as established by means of craniometric traits. American Journal of Physical Anthropology, 137, 274-282.

Varela, H. H., Cocilovo, J. A., Fuchs, M. L. & O’Brien, T. G. (2014). Coastal, Valley, and Oasis Interaction: Impact on the Evolution of Ancient Populations in the South Central Andes, American Journal of Physical Anthropology, 155, 591-599.

von Cramon-Taubadel, N., (2014). Evolutionary insights into global patterns of human cranial diversity: population history, climatic and dietary effects. Journal of Anthropological Sciences, 92, 43-77.

Wilder, H., (1920). Laboratory manual of anthropometry, Philadelphia: P. Blakiston's Son & Co.

Yacobaccio, H. D., (2012). Intercambio y Caravanas de Llamas en el Sur Andino 3000-1000 AP, Comechingonia Revista de Arqueología, 16, 31-51.

Yacobaccio, H. D., (2017). Peopling of the high Andes of northwestern Argentina, Quaternary International, http://dx.doi.org/10.1016/j.quaint.2017.01.006.