

Issues of Affinity: Exploring Population Structure in the Middle and Regional Developments Periods of San Pedro de Atacama, Chile

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ABSTRACT The Middle Period (AD 400–1000) in northern Chile's Atacama oases is characterized by an increase in social complexity and regional interaction, much of which was organized around the power and impact of the Tiwanaku polity. Despite the strong cultural influence of Tiwanaku and numerous other groups evident in interactions with Atacameños, the role of immigration into the oases during this period is unclear. While archaeological and bioarchaeological research in the region has shown no evidence that clearly indicates large groups of foreign immigrants, the contemporary increase in interregional exchange networks connecting the oases to other parts of the Andes suggests residential mobility and the possibility that movement of people both into and out of the oases accompanied these foreign

influences. Here, we analyze biodistance through cranial non-metric traits in a skeletal sample from prehistoric San Pedro de Atacama to elucidate the extent of foreign influence in the oases and discuss its implications. We analyzed 715 individuals from the Middle Period (AD 400–1000) and later Regional Developments Period (AD 1000–1450), and found greater phenotypic differences between Middle Period cemeteries than among cemeteries in the subsequent period. We argue that this greater diversity extends beyond the relationship between the oases and the renowned Tiwanaku polity and reflects the role of the oases and its different *ayllus* as a node and way station for the Middle Period's myriad interregional networks. *Am J Phys Anthropol* 152:370–382, 2013. © 2013 Wiley Periodicals, Inc.

Nestled between the Andes and the Cordillera de Domeyko, at an altitude of nearly 2,500 miles above sea level, the oases of San Pedro de Atacama provide one of the few spots of arable land in the hyper-arid Atacama Desert (Fig. 1). Resulting from their strategic location, the Atacama oases seem to have functioned as a node in trans-Andean trade networks, serving as a potentially obligatory stop for many of the caravans that linked the Chilean coast, northwest Argentina and the Bolivian altiplano (Berenguer and Dauelsberg, 1989; Núñez, 1992; Llagostera, 1996; Nielsen, 2006; Pimentel, 2009). The long distance interaction between the Atacameño oases and the Tiwanaku polity has been the focus of decades of archaeological investigation (e.g., Le Paige, 1961; Orellana, 1985; Thomas Winter et al., 1985; Torres and Conklin, 1995; Stovel, 2001; Knudson, 2008; Torres-Rouff, 2008). However, these same networks also opened up routes of communication with groups in southern Bolivia and northwest Argentina (e.g., Uribe Rodríguez and Agüero Piwonka, 2001; Núñez Regueiro and Tartusi, 2002; Conklin and Conklin, 2007).

While it is likely that most groups in the South Central Andes did not carry the social weight and potential prestige of the Tiwanaku polity (Janusek, 2004), the presence of a diverse array of material culture in the oases reflects the increasing interregional interaction that typified the Middle Period (AD 400–1000).¹ Although there is no strong case for Tiwanaku colonization in San Pedro de Atacama, there is some indication

of the occasional presence of non-local individuals (Torres and Conklin, 1995; Knudson, 2007; Torres-Rouff

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¹Here we have chosen to use the chronological determinations of Middle Period and Regional Developments Period, which broadly overlap with the more generalized Middle Horizon and Late Intermediate Period used in the pan-Andean chronology. The difference in dates between the Middle Period (AD 400–1000) and the Middle Horizon (AD 500–1000) encompass a century where, in the oases, we have evidence for large-scale interactions and Tiwanaku influence suggesting that it belongs as part of the same cultural horizon.

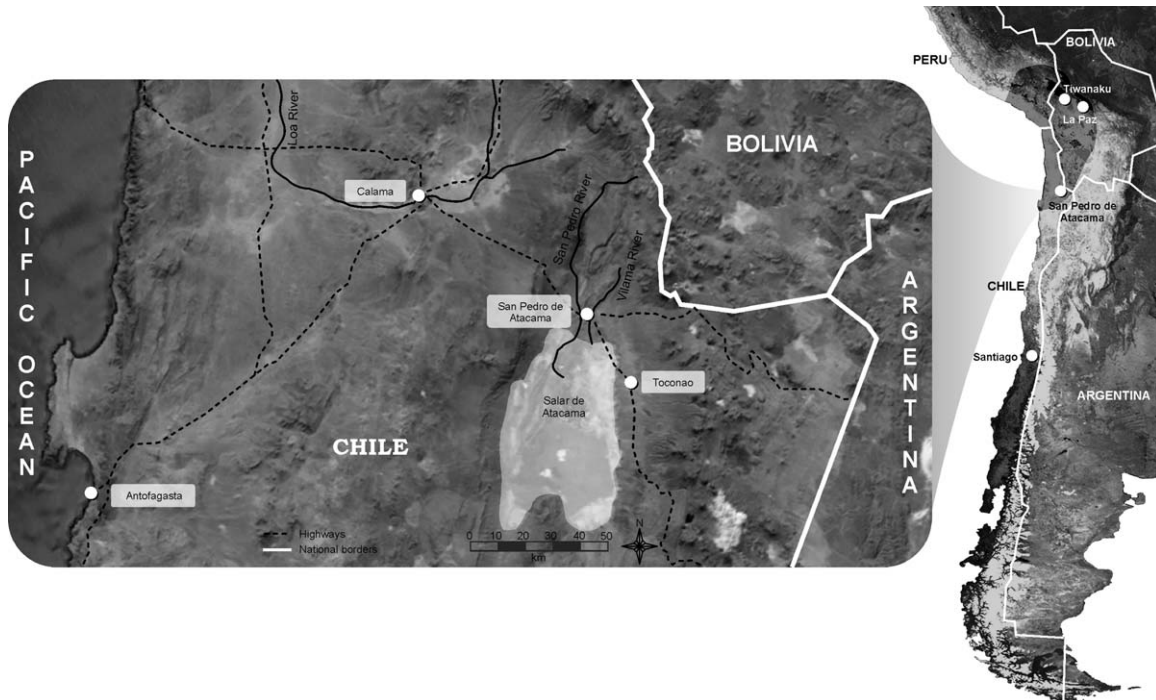


Fig. 1. Map of the south-central Andes indicating the location of the San Pedro de Atacama oases and the site of Tiwanaku.

and Knudson, 2007; Ms.). During the Middle Period, the San Pedro de Atacama oases functioned as a crossroads for numerous groups who left traces of their interactions in the form of the material goods that were carefully placed in numerous tombs.

It is worth noting that most research on the local oases to date has focused on them as unique and homogeneous entities, disregarding the potential for studying social and economic differences among the communities that inhabited the local oases. As in colonial times, present day San Pedro de Atacama is organized into geopolitical units—*ayllus*—that were likely established in pre-colonial times, as is the case throughout the Andes (Núñez, 1992; Llagostera, 2004). The *ayllu* is a traditional form of Andean kin-based community structure that represents both a political grouping and one built on lineage (ascriptive descent groups; Cock, 1981; Abercrombie, 1998). Locally, these also reflect contemporary geographic and population separations. The oases' circumscription in the landscape also makes it reasonable to assume that these geopolitical divisions were at least partially present in the past, especially in those cases where *ayllus* are physically separated from each other by open desert (Fig. 2).

The *ayllus* that comprise the Atacameño oases likely had different ties to interregional networks and foreign groups, something that is manifest in ceramics, textiles, baskets, snuff trays, and other goods (e.g., Oakland Rodman, 1992; Llagostera, 1996; Núñez Regueiro and Tartusi, 2002; Torres-Rouff, 2008). The possibility that different *ayllus* experienced different levels of interaction with an array of foreign cultures raises the question of whether and how the surge in interaction during the Middle Period affected the biological structure of the local population. If *ayllu* boundaries reflected different connections to foreign representatives, it would be expected that

any biological influx into the oases would be largely restricted to the *ayllu* in which this contact was centered over time, thus unique and differing extra-local connections are expected to increase the biological differences among *ayllus*. Furthermore, if such barriers existed during the Middle Period, the biological differences between *ayllus* likely disappeared in the subsequent Regional Developments Period with the collapse of the interregional exchange network structured around Tiwanaku.

Consequently, here we test the hypothesis that, during the Middle Period, the differential nature of the relationships between cemeteries, *ayllus*, and an array of different foreign entities resulted in an increase in the biological differences between groups in the Atacameño oases, and that these differences were subsequently lost during the Regional Developments Period. In other words, we explore the nature of the changes that an influx of foreign individuals may have had on population structure in the San Pedro de Atacama oases and whether this structure was determined to any extent by the geopolitical divisions promoted by the *ayllus*. To do so, we analyze biological distances derived from cranial non-metric traits, which provide us a window into potential biological diversity in Middle Period San Pedro de Atacama that is not tied to portable objects and shifting cultural practices.

Population diversity in the Middle Period

As archaeologists have moved away from considerations modeled on cores and peripheries there has been an increasing exploration of the spaces between centers that may have functioned as smaller nodes for managing interaction between groups; these studies have been particularly fruitful in the Andes (e.g., Upham, 1992; Nielsen, 2006; Cases et al., 2008). Nielsen (2006; p 33), in

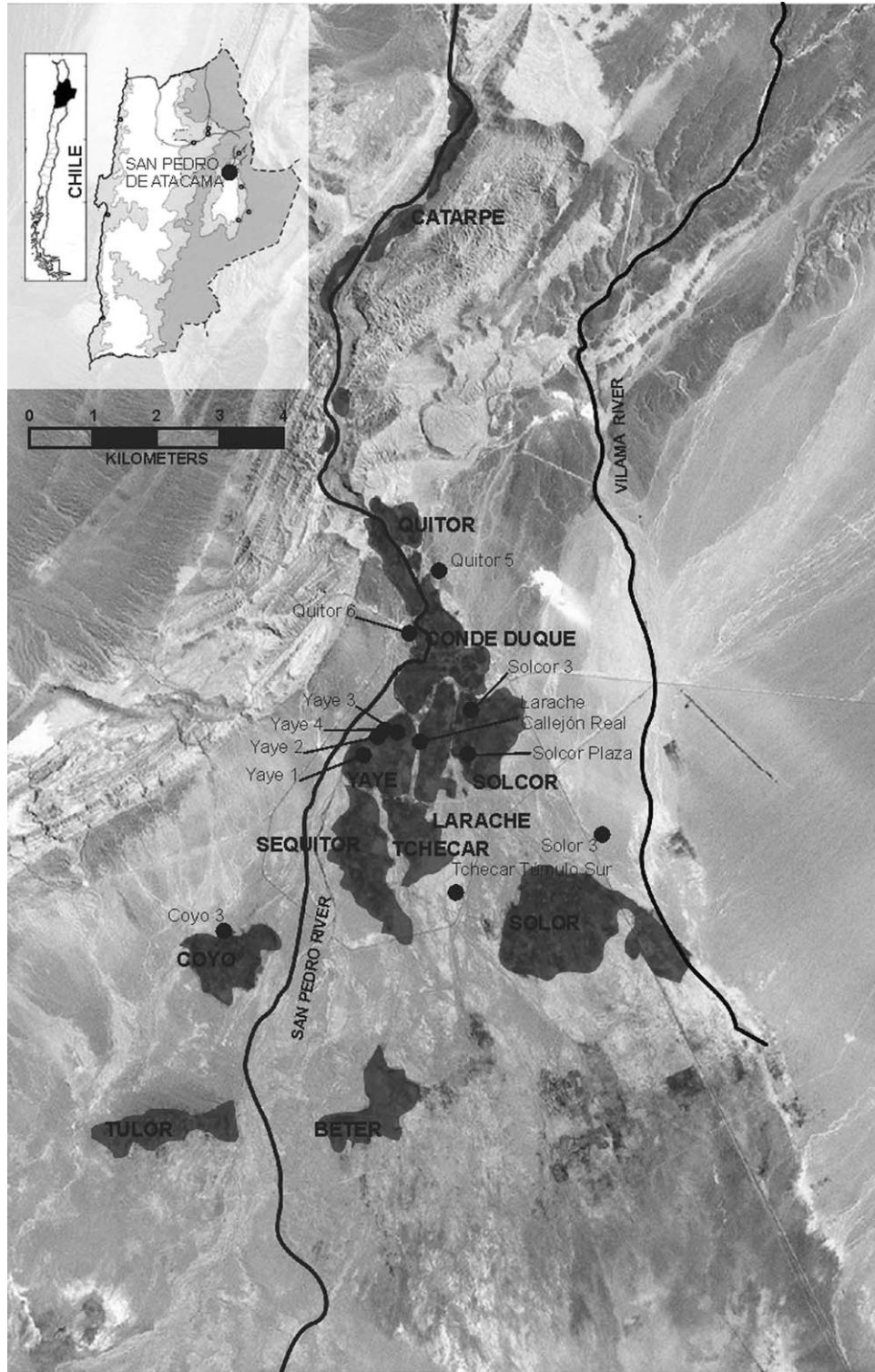


Fig. 2. Map of the San Pedro de Atacama oases indicating the location of the cemeteries studied here.

particular, stresses the value of internodal spaces for helping understand the negotiation of social relations by considering the role of individual actors. Human interactions across the Atacama Desert became prominent in the Middle and Late Formative Periods (500 BC–AD 400) (e.g., Torres-Rouff et al., 2012a,b). These ties appear

to have been strengthened with the onset of the Middle Period and its formalized exchange networks, Tiwanaku’s “state-managed llama caravans” (Janusek, 2004; p 69), and the rise of the snuff complex, which seemingly depended on *Anadenanthera* spp. brought from north-west Argentina (Torres et al., 1991).

The Middle Period was a time of substantive change in the Atacama; in addition to a rise in interactions, there was also a noted increase in prosperity associated with growing population and settlement size (Llagostera, 1996; Llagostera and Costa, 1999; Torres-Rouff and Hubbe, Ms.). Despite a range of perspectives on the potential mechanisms of interaction, a number of groups clearly interacted with the people of the Atacama at any given moment, particularly during the Middle Period (Berenguer and Dauelsberg, 1989; p 161; Oakland Rodman, 1992; p 335; Torres and Conklin, 1995; Browman, 1997; Varela and Cocilovo, 2000; Costa Junqueira et al., 2004; Stovel, 2008; Torres-Rouff, 2008; Nado et al., 2012). Numerous scholars have presented evidence for the occurrence of goods from diverse foreign groups in the Atacameño oases at this time (e.g., Oakland Rodman, 1992; Stovel, 2001; Llagostera, 2004; Conklin and Conklin, 2007). However, while there are small numbers of artifacts in non-Atacameño styles present in the oases, Middle Period cemeteries show no evidence of foreign emissaries in the form of completely distinct tomb styles, mortuary assemblages, or cultural treatments of the body (e.g., Torres and Conklin, 1995; Torres-Rouff, 2008). Furthermore, studies presenting results of radiogenic strontium isotope analyses from Middle Period cemeteries showed an overwhelmingly local population with only a few first generation migrants documented in several of the local cemeteries (Knudson, 2007, 2008; Ms.).

While archaeologists have reached the consensus that San Pedro de Atacama was not a Tiwanaku colony, this does not mean that the Middle Period did not bring with it increasing numbers of travelers who may have become part of Atacameño society and ultimately been buried there (e.g., Torres-Rouff and Knudson, 2007). Moreover, given that the Tiwanaku were not the only outside group moving through the oases at the time, it is likely that we would not see an enclave but rather an increase in the biological and cultural diversity of the area.

Supporting the archaeological information for these varied interactions in the Middle Period, craniometric data from a limited sample have shown a concurrent increase in biological variation (Varela, 1997; Varela and Cocilovo, 2000), suggesting that the Middle Period witnessed an upsurge in the movement of people into the region. Varela and Cocilovo (2000) base their research on linear craniometric measurements of a small sample of 120 crania selected from among 12 larger local cemeteries² and grouped into chronological phases based on ceramic seriation (but see Torres-Rouff and Hubbe—in press—for a current review of the local chronology). These authors use this increased craniometric variation to argue for the immigration and incorporation of a substantial number of Tiwanaku peoples into the local population (Varela and Cocilovo, 2000; p 131). A later craniometric study conducted by the same authors focused exclusively on one of the *ayllus* (Quitor) and included a larger sample of 326 skulls selected from eight cemeteries³ (Varela and Cocilovo, 2009). Neverthe-

less, the authors arrived at similar conclusions: they observe an increase of biological diversity during the Middle Period attributed to the influx of biological diversity from neighboring regions.

Recent studies have suggested that this influence was probably not restricted to individuals coming from the Tiwanaku capital, but rather, also included the movement of individuals from areas of northwest Argentina as well as neighboring Chilean cultures. For example, Costa et al. (2009) and Marsteller et al. (2011) complement this discussion of Tiwanaku and highland mobility with paleopathological evidence suggesting the movement of Atacameño women into and out of the *yungas* (the jungles of the eastern slopes of the Andes) of northwest Argentina. Both studies focus on the presence of leishmaniasis in a few female skeletons from the Atacameño oases. This is a pathology that could not be contracted in the arid climate of the Atacama, suggesting that these individuals traveled to/from at least the Argentine *yungas*, where leishmaniasis is known to occur. This coincides with the presence of material culture from this area in the oases during the Middle Period.

Together, these disparate data sets suggest that the Middle Period was a time of greater cultural and biological diversity when compared with earlier or later periods. This may reflect an influx of foreign goods as a result of Atacameño movement into new regions in addition to the oases functioning as a way station for foreign traders and travelers (Llagostera, 1996). What remains unresolved is whether and how that influx and variation is manifest in the bodies of those interred in the oases. Building on the work of other authors, including Varela and Cocilovo (2000, 2009), we provide a broader perspective on population structure in prehistoric San Pedro de Atacama by using a large sample comprised of all well-preserved adult crania from numerous cemetery excavations. Moreover, given that it is likely that different lineage groups had varied relations with distant groups, we raise the important question of whether biological diversity varied between cemeteries and/or *ayllus*.

MATERIALS AND METHODS

This analysis included the remains of 715 adult individuals interred in 12 cemeteries distributed across the oases (Table 1; Fig. 2). These span the Middle Period (AD 400–1000) through the Regional Developments Period (AD 1000–1450). Juveniles were excluded from the discrete trait analyses because of the possibility that certain cranial features are not fully developed until adulthood. Individuals of indeterminate sex were also excluded from the analysis to avoid bias in the distance calculations (see below). The resultant sample size for each cemetery is presented in Table 1. The sample was analyzed using standard bioarchaeological methods (i.e., Buikstra and Ubelaker, 1994; Buzon et al., 2005). To be considered here, a cranium needed to be over 75% complete and include the majority of the facial bones. Given that many of these cemeteries were excavated decades ago, a large part of the sample contains no postcranial elements. As such, sex was primarily determined based on the sexually dimorphic features of the skull, although the os coxae were examined when available.⁴ Individuals

²These 12 cemeteries include five cemeteries considered in this study; however, Varela and Cocilovo do not delimit the portion of their sample of 120 crania that was derived from each. From these same five cemeteries (Quitor 5 and Yaye 1-4) we include a total of 221 individuals in our study.

³This included 91 individuals from Quitor 5, a site from which we include 117 individuals.

⁴Of the 715 individuals included here, os coxae were available for the 184 individuals interred in the cemeteries of Coyo 3 ($n = 45$), Quitor 6 Tardío ($n = 35$), and Solcor 3 ($n = 104$).

TABLE 1. *The sample*

Site	Period ^a	Radiocarbon date range (cal AD) ^b	N
Solor 3	Late Formative/Middle Period	AD 83–602	49
Larache	Middle Period	AD 337–562	43
Quitor 5	Middle Period	AD 449–1019	117
Solcor 3	Middle Period	AD 781–981	104
Solcor Plaza	Middle Period	AD 436–1201	56
Tchecar Túmulo Sur	Middle Period	AD 711–1132	162
Coyo 3	Middle/Regional Developments Period	AD 897–1207	45
Quitor 6 Tardío	Regional Developments Period	AD 899–1487	35
Yaye 1	Regional Developments Period	AD 892–1260	30
Yaye 2	Regional Developments Period	AD 667–1150	36
Yaye 3	Regional Developments Period	AD 780–992	20
Yaye 4	Regional Developments Period	AD 782–1016	18
Total			715

^aLate Formative: AD 1–400; Middle Period: AD 400–1000; Regional Developments Period: AD 1000–1450. Cemetery adscription to periods follows both the available absolute chronology and indicative elements of the funerary context studied by archaeologists.

^bSee Torres-Rouff and Hubbe (Ms) for a detailed presentation and discussion of the available absolute dates. The radiocarbon range presented is derived from the small number of available ¹⁴C dates from each cemetery. Consequently, in some cases the period associated with the cemetery does not perfectly match the absolute chronology, however, in these cases the archaeological data overwhelmingly supports the period attributions.

were grouped into broad age categories (young adult, 18–30; middle adult, 30–45; old adult, 45+) based on cranial suture closure, or postcranial remains when they were available.

Nonmetric traits are minor discrete morphological features that can be readily observed and scored (on either a presence/absence basis or using a graded scale) during macroscopic analysis of skeletal remains. The variation in these features, which are found on both cranial and postcranial bones, are “innocuous minor skeletal variants . . . considered mere skeletal anomalies . . . for more than two centuries” (Hauser and De Stefano, 1989; p 1). Cranial nonmetric (or discrete) traits include small extra bones within cranial sutures (ossicles), abnormal bony projections, failures in typical ossification patterns that result in small, non-detrimental holes in a bone’s surface, and variation in the number or positions of foramina (holes for blood vessels or nerves) (Buikstra and Ubelaker, 1994; p 85). Analyses of these suites of traits have been employed in biodistance and evolutionary studies in physical anthropology with success since at least the late 1950s (Berry and Berry, 1967; Sjøvold, 1973, 1977). More specifically, bioarchaeologists frequently use these traits to assess biological relationships or patterns of genetic relatedness in archaeological populations (e.g., Droessler, 1981; Konigsberg, 1990; Sutter and Mertz, 2004; Blom, 2005).

In this study, we collected data on 21 nonmetric cranial traits (Table 2; Hauser and De Stefano, 1989; Buikstra and Ubelaker, 1994), although we used only a subset of these in the distance calculations (see below). All traits were collected by one of us (C.T.R.) and intra-observer error tests on a subsample showed no significant differences in trait analysis. Frequencies of traits for each cemetery can be seen in Supporting Information Table 1. Previous studies have presented conflicting results as to the effect of intentional cranial vault modification, a cultural practice visible in around 50% of our sample, on cranial discrete traits. The nonmetric traits selected for this project are only minimally affected by head shaping (Konigsberg et al., 1993; Verano, 2003; Rhode and Arriaza, 2006). In particular, sutural bones were not considered here as a number of studies have

suggested that ossicles and sutural complexity are particularly responsive to intentional cranial modification (e.g., Clark and Arsdale, 2007).

While the expression of cranial nonmetric traits shows only low to moderate genetic heritability (Carson 2006), they have been successfully used to discriminate biological populations in many studies (Sjøvold, 1977; Prowse and Lovell, 1996; Hanihara et al., 2003; Hallgrímsson et al., 2004), and have been shown to present similar results to those derived by other lines of evidence (Prowse and Lovell, 1996; Hanihara et al., 2003). Although dental nonmetric traits show higher heritability values, and therefore would conceivably be a better tool for estimating biological affinities between populations, the collections available from the Atacameño oases lack a sufficient number of well-preserved teeth for such analyses due to the confluence of severe attrition and a high prevalence of antemortem tooth loss, compounded with a substantial loss of teeth postmortem as a result of earlier conservation practices. Observation and scoring of nonmetric traits was made with reference to drawings and photographs. For bilateral traits, maximal expression was documented, since significant asymmetry is uncommon and this helps to maximize sample size (Berry, 1979; Sutter and Cortez, 2005). Graded (non-dichotomous) data were made dichotomous in advance of data collection (see Table 2).

Under the assumption that nonmetric cranial traits can be used to successfully study biological affinities, differences in trait frequencies between human groups would indicate overall biological differences between them. Such differences can be a result of stochastic evolutionary processes (e.g., drift and gene flow), following an isolation by distance (geographical or temporal) pattern, genetic influx via differential migration between the groups, isolation imposed by cultural behavior, or a combination of these processes. It is generally hard to separate the individual contribution of each of these effects, although useful approaches have been proposed, in particular to test isolation by (geographic and/or temporal) distances (Konigsberg, 1990). The San Pedro de Atacama oases offer an interesting situation, in which all of the cemeteries included in this analysis are within

TABLE 2. Discrete traits used in this study

Cranial trait	Description of presence of trait	Trait definition
Complete Metopic Suture	At least partial presence heading towards bregma across the frontal (but extending noticeable beyond glabella)	Hauser and DeStefano (1989; p 41–44)
Supraorbital Foramen	Foramen must be complete and unobstructed	Hauser and DeStefano (1989; p 50–55)
Supraorbital Notch	Greater than half of the notch is occluded by spicules	Buikstra and Ubelaker (1989; p 87)
Infraorbital Suture	Complete suture running from the orbital margin to the infraorbital foramen	Buikstra and Ubelaker (1989; p 87)
Absence of Zygomaticofacial Foramen	Lack of a complete and unobstructed foramen	Hauser and DeStefano (1989; p 224–225)
Multiple Zygomaticofacial Foramen	Two or more foramina must be complete and unobstructed	Hauser and DeStefano (1989; p 224–225)
Os Japonicum	A distinct suture running horizontally across the zygomatic bone dividing the zygomatic in two	Hauser and DeStefano (1989; p 222–223)
Parietal Foramen	Foramen located near obelion must be complete and unobstructed	Hauser and DeStefano (1989; p 78–82)
Tympanic Dehiscence	Incomplete closure of the tympanic portion of the temporal resulting in a clear and unobstructed perforation.	Hauser and DeStefano (1989; p 143–44)
Double Condylar Facet	Two discrete facets or one facet divided in two resembling the Figure 8	Hauser and DeStefano (1989; p 116–118)
Condylar Canal	Complete and unobstructed canal	Hauser and DeStefano (1989; p 114–115)
Divided Hypoglossal Canal	Spines dividing the canal form a complete bridge	Buikstra and Ubelaker (1989; p 89)
Complete Foramen Ovale	Foramen must be complete and unobstructed	Buikstra and Ubelaker (1989; p 90)
Complete Foramen Spinosum	Foramen must be complete and unobstructed	Buikstra and Ubelaker (1989; p 90)
Complete Pterygospinous Bridge	A complete bony bridge over the foramen spinosum	Buikstra and Ubelaker (1989; p 90)
Complete Pterygoalar Bridge	A complete bony bridge over the foramen ovale	Buikstra and Ubelaker (1989; p 90)
Pre-Condylar Tubercle	Presence of a bony tubercle located immediately anterior to the occipital condyle	Hauser and DeStefano (1989; p 134–136)
Absence of Mastoid Foramen	Lack of a complete and unobstructed foramen	Hauser and DeStefano (1989; p 201–205)
Extrasutural Mastoid Foramen	Foramen must be complete and unobstructed and located away from the suture	Hauser and DeStefano (1989; p 201–205)
Highest Nuchal Line	Arises at external occipital protuberance, arching anteriorly and laterally	Hauser and DeStefano (1989; p 104–106)
Accessory Palatine Foramen	Multiple complete and unobstructed foramina are located posterior to the palatine foramina	Hauser and DeStefano (1989; p 163–164)

Traits in bold were included in the final analyses.

walking distance of each other (the two most distant ones are less than 15 km apart, see Fig. 2), such that isolation by geographic distance would not be expected between sites. Consequently, any difference observed between sites of the same chronological period must respond to biological barriers imposed by factors other than geographic isolation (e.g., differential migration and/or socially imposed mating barriers). Since our current knowledge of cultural differences is not detailed enough to construct a predictive model to test its correspondence with biological distances, in order to test our hypothesis of increased biological differences among cemeteries in the Middle Period we adopted the more

straightforward (and exploratory) approach of testing whether there are statistical differences between trait frequencies in the cemeteries included in our analysis. In this way we are able to test our hypothesis as well as identify which cemeteries are associated with the observed differences.

Given the ongoing conversations regarding the distinct approaches used to calculate biodistances based on non-metric data (e.g., Schillaci et al., 2009; Irish, 2010), here we calculated biodistances between the cemeteries using two formulae. The first approach was to calculate distances using C.A.B. Smith's Mean Measure of Divergence (MMD; following Sjøvold, 1977). MMD has been

criticized and considered inferior to other biodistance approaches by some scholars (e.g., Mahalanobis Distance; Konigsberg, 1990), even though it tends to show high correlations with other methods (e.g., Irish, 2006, 2010; Schillaci et al., 2009). We chose to use MMD here as it offers a measurement of statistical significance that allows us to test the hypothesis that cemeteries have equal frequencies of nonmetric traits, given that MMD allows for the estimation of sample variance, which can be used to refute with an alpha of 2.5% the null hypothesis (distance = 0) for each pairwise comparison (see details and formulae in Irish, 2010). Distances were considered statistically significant if they were higher than twice the square root of the variance (Sjøvold, 1977). The MMD formula used here also incorporates a correction for sample size, which reduces the distance between groups as sample sizes decrease (Irish, 2010).

The second biodistance used here is the adapted Mahalanobis distance, as proposed by Konigsberg (1990). The Mahalanobis distance has been deemed superior to MMD (Konigsberg, 1990; Schillaci et al., 2009), since it also corrects for the correlation between traits. Although both MMD and the Mahalanobis distance derive from the same family of biodistances (Irish, 2010:380), the equation used here does not correct for sample size. Therefore, the main sources of differences between the distances used here will be the correction for sample size in the case of Smith's MMD, particularly for the smaller samples, and the correction for intercorrelation between traits in the case of Mahalanobis distance.

The graphic representation of both distances was accomplished via Multidimensional Scaling (using the Guttman-Lingoes method for the initial configuration and two dimensions as the final solution), which represents the best visualization of the relative distances between series in the two dimensions of a graph (Hair et al., 2009). By representing the biological affinities of both distance matrices, we expect to discuss patterns of relationships that are common when different biodistances are adopted: one with a tendency to underestimate distances (MMD), due to the sample size component of the equation, the other with a tendency to inflate the distances of small series (Mahalanobis), since small samples would be poor representations of the population we

are trying to estimate. Therefore, together, the two MDS graphs should represent the range of possible affinities between series.

Before the calculation of the distances and to improve comparability of the distance matrices, variables that were highly correlated (tetrachoric $r > 0.7$) were removed from the analyses, to avoid overrepresentation of trait frequencies in the final MMD distances. Sex differences within cemeteries were not accentuated, with the exception of one variable (Absence of Mastoid Foramen) that had higher frequencies in women in 6 of the 12 series. Therefore, this variable was also removed to avoid sex biases in the final results. As mentioned earlier, adults of indeterminate sex were not considered in this study. Males and females were pooled together to increase sample sizes, particularly in the Regional Developments Period cemeteries. The final list of variables used was reduced to 12 traits, as detailed in Table 2. MMD and Mahalanobis matrices were calculated using functions written for this purpose in R (R Development Team, 2012), using the polychor function from Polychor Package to calculate tetrachoric correlations for the Mahalanobis distances. MDS was performed with the complete matrix of pairwise MMDs or Mahalanobis distances in Statistica 7 (Statsoft, Inc.). The MDS goodness of fit was represented via stress measurement and also graphically via Shepard diagrams.

RESULTS

Table 3 presents the MMD values between all pairs of cemeteries, and highlights those values considered statistically significant ($P \leq 0.025$). Within the Regional Developments Period no distances are significant between the cemeteries, whereas many of the distances between sites from the Middle Period are considered statistically different from 0, supporting our hypothesis that during the Middle Period differential migration and/or cultural isolation processes accentuated biological differences between cemeteries. However, these results must be considered with caution due to the fact that Regional Developments Period sites have smaller sample sizes and therefore the sample size correction included in the MMD formula used here will make it harder to

TABLE 3. MMD values (below diagonal) and variance (above diagonal)

		Middle period						Regional developments period					
		Solor 3	Larache	Quitor 5	Solcor 3	Solcor Plaza	Tchecar T. S.	Coyo 3	Quitor 6 Tardío	Yaye 1	Yaye 2	Yaye 3	Yaye 4
Middle Period	Solor 3		0.024	0.015	0.016	0.019	0.014	0.023	0.025	0.025	0.023	0.033	0.035
	Larache	0.094		0.017	0.018	0.021	0.016	0.025	0.027	0.027	0.025	0.035	0.036
	Quitor 5	0.071	0.027		0.009	0.012	0.007	0.016	0.018	0.018	0.016	0.026	0.028
	Solcor 3	0.021	0.006	0.050		0.012	0.007	0.017	0.019	0.019	0.017	0.027	0.028
	Solcor Plaza	0.035	0.000	0.034	0.005		0.011	0.020	0.022	0.022	0.020	0.030	0.032
	Tchecar T. S.	0.023	0.034	0.022	0.007	0.029		0.015	0.017	0.017	0.015	0.025	0.026
Regional Developments Period	Coyo 3	0.021	0.120	0.127	0.061	0.064	0.065		0.026	0.026	0.024	0.034	0.036
	Quitor 6	0.151	0.109	0.110	0.104	0.130	0.130	0.129		0.028	0.026	0.036	0.038
	Tardío												
	Yaye 1	0.105	0.036	0.089	0.063	0.025	0.106	0.086	0.005		0.027	0.037	0.038
	Yaye 2	0.148	0.060	0.113	0.092	0.077	0.116	0.134	0.008	0.000		0.034	0.036
	Yaye 3	0.203	0.136	0.195	0.112	0.159	0.157	0.110	0.000	0.009	0.010		0.046
	Yaye 4	0.000	0.031	0.044	0.007	0.000	0.026	0.009	0.001	0.000	0.000	0.038	

MMD values in bold are significant at $P \leq 0.025$.

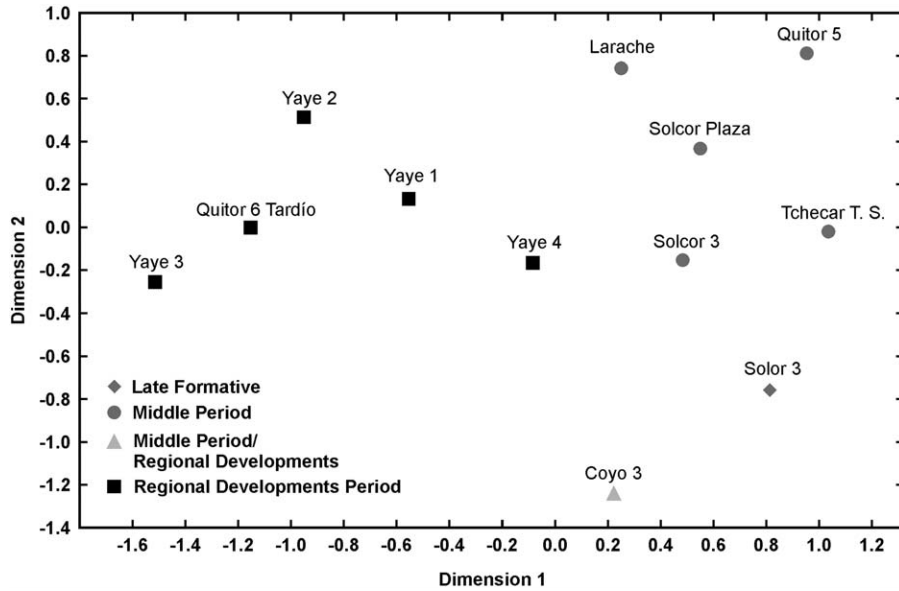


Fig. 3. Multidimensional scaling solution of standardized Mean Measure of Divergence values (stress: 0.108; Number of iterations: 16).

refute the null hypotheses for distances that include these sites.

In contrast, distances between periods are all statistically significant, with the exception of the distances to Yaye 4 and two of the distances to Yaye 1, which suggests that time is playing a major role in the overall biological differentiation for the cemeteries included in this study. The relationship between the cemeteries can be better observed in the Multidimensional Scaling plots. Figure 3 shows the MDS plot (stress for the two dimensions = 0.108) based on the MMD distance matrix (Table 3) while Figure 4 shows the MDS plot (stress for the two dimensions = 0.085) based on the Mahalanobis distance matrix (Table 4). In both plots, the strongest separation between samples is given by the temporal differences,

with samples from the Regional Developments Period clustering together and distant from the Middle Period samples. The fact that the MDS based on the Mahalanobis distances (without a sample size correction) also shows the Regional Developments Period cemeteries clustered together gives further support to the lack of differences in the later period, despite the smaller sample sizes. For the cemeteries of the Middle Period, the two MDS plots show many similarities as well in the relative position of the cemeteries. In both graphs, Coyo 3—which dates to the end of the Middle Period—and Quito 5 appear separated from the remaining series, with this outlier position being more accentuated in the MDS based on Mahalanobis distances (Fig. 4). Larache stands out in the MMD analysis (Fig. 3) and Tchecar T.

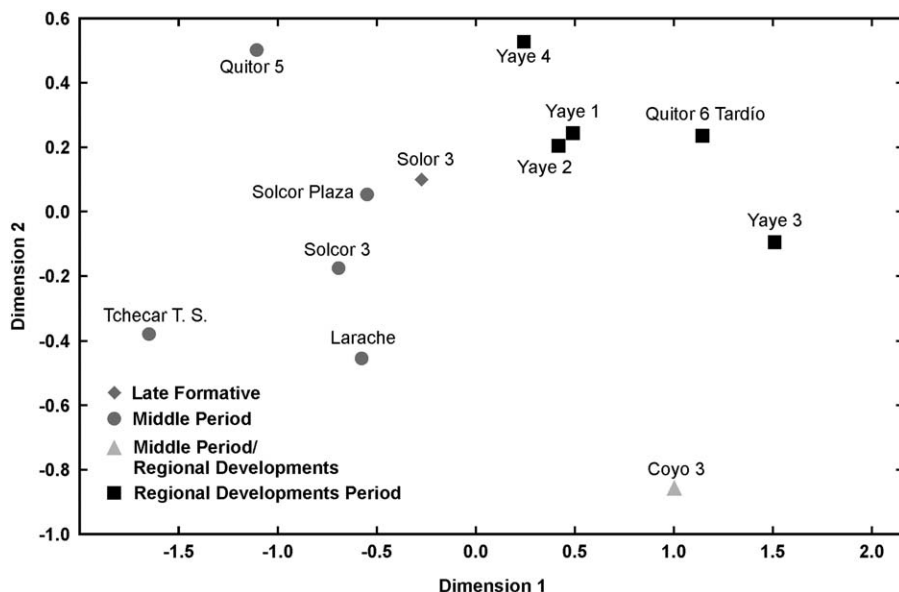


Fig. 4. Multidimensional scaling solution of Mahalanobis distances (stress: 0.085; Number of iterations: 34).

TABLE 4. Mahalanobis distances between series

MMD		Middle Period					Late Intermediate Period						
		Solor 3	Larache	Quitor 5	Solcor 3	Solcor Plaza	Tchecar T. S.	Coyo 3	Quitor 6 Tardío	Yaye 1	Yaye 2	Yaye 3	Yaye 4
Middle Period	Solor 3												
	Larache	0.229											
	Quitor 5	0.200	0.170										
	Solcor 3	0.267	0.445	0.595									
	Solcor Plaza	0.090	0.117	0.188	0.431								
	Tchecar T. S.	0.110	0.059	0.120	0.420	0.051							
Late Intermediate Period	Coyo 3	0.309	0.185	0.164	0.600	0.225	0.286						
	Quitor 6	0.302	0.421	0.489	0.225	0.471	0.369	0.682					
	Tardío												
	Yaye 1	0.248	0.163	0.308	0.314	0.280	0.189	0.466	0.064				
	Yaye 2	0.197	0.240	0.364	0.311	0.254	0.147	0.487	0.150	0.000			
	Yaye 3	0.414	0.455	0.682	0.227	0.478	0.465	0.702	0.124	0.156	0.185		
	Yaye 4	0.120	0.297	0.352	0.321	0.228	0.162	0.530	0.190	0.100	0.074	0.322	

S. appears as another outlier in the Mahalanobis MDS (Fig. 4). The remaining samples generally occupy the center of the distribution of the Middle Period cemeteries in both analyses.

DISCUSSION

Our results tend to support the hypothesis that during the Middle Period, *ayllu* organization played a stronger role in keeping local groups biologically distinct when compared with the population during the Regional Developments Period. However, the differences observed between Middle Period cemeteries were not as pronounced as the differences accumulated over time, since the major differentiation we observe (Figs. 3 and 4) is a result of the period adscription of the cemeteries. This scenario suggests that the large amount of interaction documented in the archaeological record during the Middle Period is, to some degree, also reflected in the biological diversity of the population. As addressed briefly above, increased distance between groups of the Middle Period, here reflected in the different frequencies of analyzed traits, can derive from two complementary processes: 1) influx of individuals with different biological backgrounds (in this case, different frequencies of non-metric traits), whose arrival in the new population results in a change in trait frequency; and 2) prolonged isolation between *ayllus*, which over generations will tend to accentuate differences originally present between them (Hartl and Clark, 2006). Influx of new (and genetically distinct) individuals is the fastest and most efficient way to change the genetic makeup of a population, and is usually considered the main force behind biological (or morphological) differences between populations. However, any new genetic variability brought in by migration will only impact a population if the number of individuals migrating represents a significant portion of the population that is receiving them (Hartl and Clark, 2006). This can either be achieved through significant gene flow (migration of a large number of individuals at one time or several smaller migrations over prolonged periods of time), which would, however, reduce the variation among groups receiving the immigrants, or restricting gene flow to a smaller part of the population as smaller groups will facilitate the fixation of new genes as a result of stochastic processes (Hartl and Clark, 2006). Consequently, biological differences observed

between prehistoric populations such as the ones studied here should be interpreted as a result of the combination of migration (in our case, migration from the Tiwanaku area and other south-central Andean communities) and the degree of isolation between groups based on amount/presence of gene flow. Since, in this case, geographic distances cannot be considered as a reasonable factor for isolation between groups of the same time period given the proximity between sites, isolation in this case (if present) must have resulted from cultural practices. As such, more biological differences would be expected if the foreign influence in the Atacameño oases was restricted to a few groups who maintained stronger ties with outside groups and also maintained a degree of genetic isolation from neighboring *ayllus* due to, for example, increasing social hierarchy reflected in stronger inequalities or occupational specialization between groups.

Given the existence of ample trade networks, the presence of individuals, and material culture from varied locations, the concomitant rise in biological diversity is not surprising (Varela and Cocilovo, 2000, 2009). While this likely suggests the influence of the Tiwanaku polity at this time (Torres and Conklin, 1995; Torres-Rouff, 2008), it also supports the idea that San Pedro de Atacama served as a node in the circulation networks of this time (Llagostera, 1996; Nielsen, 2006). Much like the ideas proposed by Nielsen (2006) concerning the importance of spaces between centers, the Atacameño oases, while never of the size or importance of the Tiwanaku heartland, clearly increased their interaction with at least this node during the Middle Period (e.g., Torres and Conklin, 1995; Llagostera, 1996; Torres-Rouff, 2008), and the biological distinction visible at this time may reflect the oases' growing role as a stopover for foreign individuals between centers. Moreover, it is possible that the Middle Period witnessed a shift, as the Atacameño oases themselves became a small node in interregional exchange networks. This would highlight the growing prominence of some of the *ayllus* after having functioned as an internodal space during the preceding Formative Period, which was dominated by the large centers in the Calama oases located some 100 km to the west (e.g., Thomas Winter et al., 1994).

The MDS plots do not demonstrate a radical break between Middle Period sites; instead, there are simply more significant differences between them when

compared to the later cemeteries. Supporting this as a trend then, we have no evidence of large-scale population movements or of the use of cemeteries by whole groups of foreigners (Knudson, 2007; Knudson and Torres-Rouff, Ms.). Even cemeteries with the highest numbers of artifacts from Bolivia and Argentina, like Larache, Coyo Oriental, and Solcor 3, exhibit very few individuals with isotopic evidence of geographic origins from outside of the Atacameño oases (Knudson, 2007). Perhaps this suggests that the differences we see are more closely related to the movement of small groups of people from various regions, rather than large state-directed population movements from the Lake Titicaca Basin. For example, while there are some individuals with radiogenic strontium isotope values consistent with geographic origins in the Lake Titicaca Basin, others likely originated in the southern altiplano or possibly northwest Argentina (Knudson and Torres-Rouff, Ms.). A case in point is the Tchecar Túmulo Sur cemetery where most individuals appear isotopically local to San Pedro de Atacama, although there are small numbers of individuals who exhibit a variety of radiogenic strontium isotope values in enamel and/or bone (Knudson and Torres-Rouff, Ms.). While we interpret the enamel values as evidence of non-local geographic origins, we interpret the elevated bone values in individuals who were originally from the Atacameño oases as possible evidence of caravaneers who moved between different geologic zones over the course of their lives.

Nevertheless, it is important to consider the possibility that some of the significant differences we see in the Middle Period may result from an increase in isolation between the *ayllus* during this time. *Ayllus* in the Andean world function as kin/fictive kin groupings that carry social weight (e.g., Abercrombie, 1998; Goldstein, 2009). The contemporary occupation of the San Pedro de Atacama oases is still organized around these groupings and they can be used, with caution, as a means of exploring possible *ayllu* patterning in the past. With the beginnings of social differentiation and the rise of local elites (e.g., Llagostera, 1996; Tamblay, 2004) it is possible that members of particular *ayllus* occupied a social role that brought them together. Among other patterns, we have noted some significant differences between *ayllus* in the practice of cranial modification that may also suggest the independent development of the constituent local communities (Torres-Rouff, 2008, 2009). For example, we have noted that sites more typically associated with Tiwanaku influence (e.g., Larache, Solcor 3) have lower rates of annular or circumferential cranial vault modification than contemporary sites with less evidence of foreign influx (e.g., Tchecar Túmulo Sur) (Torres-Rouff, 2008).

The biological differences that we document in the Middle Period appear to disappear in the subsequent Regional Developments Period. This may be tied to the loss of interregional networks and pan-Andean contacts characteristic of the tumultuous Regional Developments Period in concert with the collapse of organizing bodies like the Tiwanaku polity. During this time we likely see the maintenance and even strengthening of local ties. Our data demonstrate no significant differences between the Regional Developments Period sites. Overall, the data from the Regional Developments Period, while more limited in size and scale, suggests a reduction or perhaps assimilation of the differences between *ayllus*, associated with a decrease in migration and/or relaxation of the cultural isolation.

With the objective of creating a better dialogue between our results and previous archaeological and bioarchaeological work, here we highlight Middle Period sites of particular interest and contextualize this information within the archaeological evidence.

Population structure during the Middle Period

The earliest site considered here is Solor 3, which is transitional between the Late Formative and the Middle Period (c. AD 400). While Solor 3 is not significantly different from four of the Middle Period sites (both Solcor cemeteries as well as Tchecar Túmulo Sur and Coyo 3), it is significantly different from the early Middle Period sites of Quito 5 and Larache. If we consider the possibility that as a Late Formative/Middle Period site, Solor 3 might represent the local genetic background, the fact that some of the early Middle Period sites differ significantly from it might indicate influx or evidence of isolation early in the Middle Period. Moreover, it might serve as evidence that any influx of variation in this period was not evenly distributed across the *ayllus*. An early onset to the diversity of the Middle Period would, in turn, imply that the movement of peoples was not exclusively tied to the solidification of the caravan system with the growth of Tiwanaku polity in the late 400s (Torres-Rouff and Hubbe, in press). There are documented interactions between Atacameños and neighboring groups prior to Tiwanaku expansion as material culture from San Pedro de Atacama is found outside the oases and material from elsewhere in Atacameño graves (Berenguer et al., 1988). Taken together this suggests the importance of pre-existing ties to southern Bolivia and northwest Argentina and strengthens the argument for diversity in the oases as opposed to supporting a monolithic Tiwanaku presence.

Radiocarbon dates from Larache suggest that the cemetery was in use during the earlier part of the Middle Period (Torres-Rouff and Hubbe, in press). Larache is significantly different from many of the Middle Period sites in this analysis (Coyo 3, Solor 3, and Tchecar Túmulo Sur) and is situated at the upper margin in the MDS based on MMD (Table 3; Fig. 3). At Larache we have evidence to support this distinction in the form of first generation migrants into the area, a plethora of unique artifacts, and a handful of visibly distinct elite burials. Our recent study integrating bioarchaeological, biogeochemical, and archaeological evidence shows that Larache served as a burial place for a diverse, yet culturally integrated, potentially elite and well-connected segment of the Atacameño population (Torres-Rouff et al., Ms.). The mortuary context for Larache predominantly reflects the standard pattern for the oases but also includes a series of burials with abundant metals, Tiwanaku-style artifacts, and most importantly, very few other objects (Torres-Rouff et al., Ms.). This mortuary practice is distinct, as individuals with Tiwanaku goods in other cemeteries are generally interred with substantial mortuary wealth (Torres-Rouff, 2008). In addition, radiogenic strontium isotope values show the presence of multiple first generation migrants at Larache. Of the 34 samples from 18 individuals buried at Larache that were analyzed for radiogenic strontium isotope values, five individuals displayed $^{87}\text{Sr}/^{86}\text{Sr}$ values that were not within the "local" range for San Pedro de Atacama (Torres-Rouff et al., Ms.). Larache is, therefore, the most heterogeneous of the Middle Period Atacameño

cemeteries, with mean $^{87}\text{Sr}/^{86}\text{Sr}=0.70986\pm 0.00335$ ($n=38$); in contrast, the most isotopically homogenous Middle Period Atacameño cemeteries, Coyo Oriental and Coyo 3, exhibit mean $^{87}\text{Sr}/^{86}\text{Sr}=0.70771\pm 0.00024$ ($n=17$) and mean $^{87}\text{Sr}/^{86}\text{Sr}=0.70765\pm 0.00023$ ($n=18$), respectively (Knudson and Torres-Rouff, Ms.). Interestingly, at Larache, both “local” and “non-local” individuals, as determined by radiogenic strontium isotope analyses, had access to this—perhaps elite—differentiated burial context, suggesting it was not foreignness *per se* that served as a determining factor in this burial practice. A similar pattern occurs in other Middle Period cemeteries, where individuals identified as “non-local” based on radiogenic strontium isotope values in enamel and/or bone cannot be distinguished based on burial practices or artifact styles Ms. Finally, though there are a number of Tiwanaku-style artifacts in the Larache cemetery, radiogenic strontium isotope analysis points to a number of different geographic origins in the Lake Titicaca Basin and southern altiplano, rather than a group of individuals from the Tiwanaku capital Ms.

The remaining Middle Period cemeteries display considerable diversity within and between themselves, with numerous significant differences in MMDs (Table 3). Solcor Plaza stands out as the Middle Period site with the least number of significant differences when compared to contemporary sites (Table 3). Previous studies of Solcor Plaza have shown only minimal evidence of foreign interaction in the mortuary context, a factor that may be tied to lower social standing for the individuals buried here (Torres-Rouff, 2011; Nado et al., 2012). Therefore, the fact that Solcor Plaza is not different from Solor 3 favors the idea that this cemetery might represent a population composition without a significant influx of foreign individuals. Considering this scenario we would have expected that Solcor 3, an elite cemetery with clear presence of Tiwanaku objects in many of its tombs, would display differences from Solcor Plaza; however, this may support our recent contention that social inequality, rather than foreignness, may have played an important role in segregating oases populations (Torres-Rouff, 2011, Hubbe et al., 2012). While Solcor 3 and Solcor Plaza exhibit variability in mortuary assemblages, with Solcor 3 clearly being more elite, both cemeteries are isotopically similar and do not show significant differences in the geographic origins of the individuals interred in the two cemeteries (Knudson, 2007; Ms.).

The significant differences between Quitor 5 and the other Middle Period sites are more difficult to contextualize. While there is a greater geographic distinction between the Quitor cemeteries (found north of the main cluster of oases in the San Pedro River canyon; Fig. 2), this difference is not large enough to be considered an isolation factor and there are no significant cultural differences in the mortuary context that would suggest a clear social differentiation between the sites. This may represent further evidence of social isolation between *ayllus* in this period, in concert with the increasing diversity resulting from population movement at this time. Radiogenic strontium isotope analysis may support this hypothesis; at Quitor 5, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.70790 \pm 0.00049$ ($n = 29$), which we interpret as one of the more homogeneous Middle Period cemeteries in the oases in terms of geographic origins and in contrast to the most isotopically heterogeneous cemetery, Larache, where mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.70986 \pm 0.00335$ ($n = 38$) (Knudson and Torres-Rouff, Ms.).

Finally, the clear outlier position of Coyo 3 is difficult to explain at the moment beyond its temporal association. Coyo 3 is a cemetery that was in use at the end of the Middle Period and early in the Regional Developments Period, with burial contents of diminished quality and quantity, although some slight influence from the Tiwanaku polity has been documented (Costa and Llagostera, 1994). However, Coyo 3 is the site with most significant differences with Middle Period and Regional Development sites, appearing as an outlier in both MDS analyses. Neither the archaeological work nor the bioarchaeological studies to date offer us potential hypotheses to why Coyo 3 shows this outlier position in our analysis, and this is something that should be further explored, possibly by including other Coyo cemeteries in a similar analysis.

Population structure during the Regional Developments Period

Comparing the data from the Middle Period to the Regional Developments Period, we suggest that biological differentiation decreases over time, a fact that may be tied to the general decrease in material wealth across the region as well as the collapse of the Tiwanaku polity as an organizational force. It is possible that the pattern we see in the Regional Developments Period results from the assimilation and homogenization of the Atacameño population during and after the Middle Period. Given that there is no evidence for large-scale population movement in the Middle Period, a decrease in migrants as well as in interregional interactions would imply that the variability that characterized the Middle Period would slowly be incorporated into the Regional Developments Period population. Lessening isolation between *ayllus* could also accelerate this effect. The Middle Period seems to have had a more defined and elaborate social hierarchy than seen previously or subsequently (Llagostera, 1996; Torres-Rouff, 2011; Hubbe et al., 2012). This may have served to accentuate social divisions and isolation between *ayllus*. In this case, the rupture of the social hierarchy associated with the end of the Middle Period and the concurrent collapse of Tiwanaku and the reduction in interregional networks would likely serve to equalize the earlier patterns of biological differentiation.

CONCLUSION

We argue that the cultural changes affiliated with the Middle Period played out in the biological sphere as well. The diverse array of interregional contacts and San Pedro de Atacama's changing role as a node and internodal space in these networks is paralleled by increased levels of biological differences between groups buried in the cemeteries of the period. While the data thus far are clear in demonstrating that there was not an enclave of Tiwanaku emissaries living in the oases, it is likely that individuals from the *altiplano* as well as other areas made their home in the Atacama oases during the Middle Period (Torres-Rouff and Knudson, 2007), contributing to the breadth of material culture found in local cemeteries, and seemingly also to the biological diversity of the population. While there is evidence of occasional migrants from the Lake Titicaca Basin and elsewhere, what stands out in the radiogenic strontium isotopic data mentioned above as well as in studies of the mortuary context (e.g., Stovel, 2001; Torres-Rouff, 2008) is

that Tiwanaku influence, while visible and potentially elite, was not a dominant source of foreign influence in the oases and that local culture and people were a prevailing presence. We would argue that the picture is much more expansive than Tiwanaku and reflects a diverse range of interaction between Atacameños and a number of outside groups as well as substantial variability in internal relationships.

Taking a broader view of the situation in the oases during the Middle Period, our data highlight the presence of foreign individuals and more importantly, the role of the oases as a potential way station and connection between other regional centers. This type of inter-nodal site reveals the potential for studying spaces and crossroads and the human role therein. The large volume of interregional interaction during the Middle Period is manifest not only in the objects entering the oases, but also at some level in the bodies of the population. What emerges as particularly interesting are the differences among the cemeteries and *ayllus* themselves, which may reflect the growth of internal social differentiation in the Middle Period and speak to the potential for integrative work that considers mortuary archaeology more closely.

In terms of studying population structure and change in a period of increasing foreign influence, we argue that a model that incorporates multiple lines of evidence allows us to more closely approximate patterns of population movement and internal changes. By interpreting biodistance data and population affinity in concert with contextual information and isotopic data on geographic origins, we are able to provide a more nuanced view into the ways in which biological diversity manifested in this population during the Middle Period.

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