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# Population Genetic Structure of Traditional Populations in the Peruvian Central Andes and Implications for South American Population History

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# **Population Genetic Structure of Traditional Populations in the Peruvian Central Andes and Implications for South American Population History**

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**Keywords: MtDNA; Y-CHROMOSOME; SOUTH AMERICA; PERÚ**

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**Abstract.** Molecular-based characterizations of Andean peoples are traditionally conducted in the service of elucidating continental-level evolutionary processes in South America. Consequently, “western” Andean population genetic variation is often represented in relation to “eastern” variation among Amazon and Orinoco River Basin populations. This west-east contrast in patterns of population genetic variation is typically attributed to large-scale phenomena, such as dual founder colonization events and/or differing long-term microevolutionary histories. However, alternative explanations that consider the nature and causes of population genetic diversity *within* the Andean region remain underexplored. Here we examine population genetic diversity in the Peruvian Central Andes using mtDNA HVI and Y-chromosome STR data from 17 newly sampled

populations combined with published samples. Using this geographically comprehensive data set, we first re-assess the currently accepted pattern of western vs. eastern population genetic structure, which our results ultimately reject: mtDNA population diversities were lower, rather than higher, within Andean versus eastern populations, and only highland Y-chromosomes exhibited significantly higher within-population diversities compared to eastern groups. Multiple populations, including several highland samples, exhibited low genetic diversities for both genetic systems. Second, we explore whether the implementation of Inca state and Spanish colonial policies starting at about A.D. 1400 could have substantially restructured population genetic variation, and consequently constitute a primary explanation for the extant pattern of population diversity in the Peruvian Central Andes. Our results suggest that Peruvian Central Andean population structure cannot be parsimoniously explained as the sole outcome of combined Inca and Spanish policies on the region's population demography: Highland populations differed from coastal and lowland populations in mtDNA genetic structure only; highland groups also show strong evidence of female-biased gene flow and/or effective sizes relative to other Peruvian ecozones. Taken together, these findings indicate that population genetic structure in the Peruvian Central Andes is considerably more complex than previously reported and that characterizations of, and explanations for, genetic variation may be best pursued within more localized regions and defined time periods.

Since at least the 1960s, characterizations of Andean peoples from a molecular perspective have been conducted peripherally, as part of larger investigative efforts in South America as a whole. These efforts have had two main goals: first, to inform debates on the peopling of South America and of the Americas *writ large*; second, to contribute to broad understandings of human micro- to macro-evolutionary change. Both goals were vitalized by the work of James V. Neel, Francisco M. Salzano, and associated colleagues among tribal groups in Venezuela and Brazil. Thus, from the 1960s into the 1990s, researchers working in South America conducted numerous regional studies based on “classical” markers (blood groups and proteins), primarily among peoples from the Amazon and Orinoco River Basins (e. g., Matson et al. 1966; Neel 1970; Salzano et al., 1973; Salzano et al. 1974; Ward et al., 1975; Salzano et al. 1977; Neel 1978a,b; O’Rourke and Suarez 1985), and only occasionally among peoples in the Andean region (Best et al. 1966; Matson et al. 1966; Modiano et al. 1972).

It was not until the late 1980s that researchers began to explicitly focus on the genetic history and structure of Andean peoples. Rothhammer and Silva (1989) were the first to argue for a distinct Andean pattern of biological variation as ascertained via craniometric isoline maps; this interpretation was supported by follow-up studies of craniometric and classical marker data (Rothhammer and Silva 1990, 1992; Cavalli-Sforza et al. 1994). Beginning in the early 2000s,

spatial analyses of molecular data revealed that Andean populations contain a pattern of high within- and low between-population genetic variation as compared to populations in the Amazon and Orinoco River Basins, which appear to harbor much higher levels of between-group variation (Luiselli et al. 2000; Simoni et al., 2000; Tarazona-Santos et al., 2001; Fuselli et al., 2003).

Subsequently, a distinction between “west” (i.e., the Andean mountain range and surroundings regions) and “east” (i.e., Amazonian lowlands and surrounding regions) has prevailed in discussions of continental South American population genetic variation (e.g., Pucciarelli et al. 2006; Lewis et al. 2007a; Wang et al. 2007; Lewis and Long 2008; Lewis 2009; Yang et al. 2010). This dichotomized representation of South American population genetic variation has had, in turn, important implications for the reconstruction of the continent’s early population history. Whereas some researchers view the contrasting patterns as the outcome of two distinct initial colonizing events (Luiselli et al. 2000; Rodríguez-Delfin et al. 2001), others posit that the two regions experienced differing population histories only after the initial entry into South America through the Panamanian isthmus (Tarazona-Santos et al. 2001; Fuselli et al. 2003; Rothhammer and Dillehay 2009; Yang et al. 2010; Bodner et al. 2012).

However, the above characterization of Andean diversity may be incomplete, for three reasons. First, it derives from a small number of population samples, most of which contain few individuals. Until recently, only fourteen

western Andean populations have been represented in the scholarly literature; these populations are spread over more than 4,000 km ranging from Ecuador, to Peru, northwest Argentina, and northern Chile. Many of the post-1990s molecular studies are based on repeated genotyping efforts of an even smaller set of population samples (e.g., Luiselli et al. 2000; Simoni et al. 2000; Tarazona-Santos et al. 2001; Fuselli et al. 2003; Battilana et al. 2006; Scliar et al. 2012; Roewer et al. 2013). Second, most relevant studies are based on *either* mitochondrial DNA (mtDNA) *or* Y-chromosome polymorphisms, which, in isolation, contain limited information about amounts and patterns of diversity (cf., Lewis and Long 2008).

A third weakness of the current perspective is that views on the nature and causes of population genetic diversity *within* the western Andean region of South America remain underdeveloped. This is despite the fact that archaeological and ethnohistorical studies attest to complex and varying human-environment interactions through time and space in the Andes (Sandweiss et al. 2001; Wernke 2007; Gosling and Williams 2013). Specifically, early patterns may have been most recently overlaid by Inca state practices, and later, by Spanish colonial-driven policies. For example, Inca rulers routinely moved individuals (males and females) and entire families, often throughout locales in the mountainous highlands (e.g., Matienzo 1967 [1567]; Cieza de León 1985 [c. 1550]; Wightman 1990), but also throughout the coast and areas to the south of the Titicaca Basin (Covey and Elson, 2007). Subsequent European invasions commencing in the



1530s precipitated the rapid decline of many indigenous coastal communities, whereas highland communities had higher initial rates of survival and were used for long-distance service (tributary) activities (Cook 1980). The Spanish conquest reinforced a frontier between the highlands and the Amazon Basin, while colonial policies indirectly encouraged population mixture and migration within the Andean region. Thus, the expected cumulative outcome of these phenomena on present-day indigenous population diversity is an overall maintenance of genetic variation combined with a pronounced lack of population structure throughout the region, particularly in the highland regions. It is therefore possible that the region's extant pattern of population genetic variation is best explained by events from the last half millennium, instead of or in addition to early migratory phenomena.

Given the current paucity of genetic data representing Andean indigenous peoples, we may have an unclear picture of the structure of Andean population genetic diversity, including the role of post-peopling events in shaping this structure (Pucciarelli 2006; Dillehay 2009). This study re-examines Andean genetic diversity using *both* mtDNA and Y-chromosome data from a large sample of traditional populations from within the Peruvian Central Andes, a region that includes the coast and highlands of Perú, as well as the tropical forest that begins on the eastern slopes of the Andes and descends to the Amazon Basin (von Hagen and Morris 1998:14).

Our study contributes 17 population samples from multiple ecological zones (highlands, coast, and lowlands) associated with broad cultural patterns revealed by archaeological, ethnohistorical, and ethnographic studies (c.f., D’Altroy 2015). We investigate the region’s population genetic structure to test the following two hypotheses: First, in response to previous characterizations of population genetic diversity, we test the hypothesis that populations throughout the Peruvian Central Andes in general, and highland areas in particular, show little or no population genetic structure in the form of high within- and low-between population genetic variation relative to eastern regions of South America. Second, we test whether extant patterns of variation within the Peruvian Central Andes can be parsimoniously explained by events from the last half millennium. Given that both Inca and Spanish policies were strongly implemented among all individuals (i.e., both males and females), primarily within highland communities, we explore (a) whether the pattern of genetic structure differs between highland, versus coastal and lowland, communities in the Peruvian Central Andes, and (b) whether any sex biases in patterns of variation can be detected.

## **Materials and Methods**

**Population Samples.** This study is based on multi-locus genetic data from samples collected through an international collaborative effort within the

Republic of Perú between 2001 and 2005. ACS moved from the University of New Mexico (UNM) to Arizona State University (ASU) during the course of the project. Institutional Review Boards (IRB) from both UNM and ASU approved the project, as well as from the Universidad Nacional Mayor de San Marcos (UNMSM) and the Universidad Ricardo Palma (URP), Lima, Perú. Biological samples in the form of buccal cells or blood spots were collected with informed consent from 611 individuals from 17 populations distributed throughout nine of 25 *Regiones* (first-level political and administrative subdivisions) and three ecological contexts in Perú (Fig. 1).

The Andes range defines a succession of ecozones running from the Pacific coastal desert, across areas of montane valleys and high tundra, and onto the humid eastern slope that descends to the Amazon Basin. Although mindful of the considerable local environmental diversity of the Andean region, we have found it useful to group our samples into three regions: coastal (areas lying to the west of the Andes), highland (areas lying in the mountain valleys) and lowland (areas lying in the humid tropics of the eastern escarpment).

Populations were assigned sample names according to the city, village, or locale from which individual biological samples were taken (Table 1; Fig. 1). We adopt a geographically based nomenclature given that the samples reflect relatively vulnerable populations, therefore warranting a level of conservatism in

community identification (c.f., Obregón-Tito 2013). Each individual in the sampled populations was from one of three ecological contexts: coast ( $n=78$ ), highlands ( $n=430$ ), and lowlands ( $n=103$ ). Individuals in the coastal sample were from Caleta Santa Rosa ( $n=31$ ), Catacaos ( $n=16$ ), Isllilla ( $n=18$ ), and Trujillo ( $n=13$ ). Individuals in the highlands sample were from Ancash ( $n=73$ ), Andahuaylas ( $n=56$ ), Cara Cara ( $n=26$ ), Cusco-North ( $n=34$ ), Cusco-South ( $n=95$ ), Huancapi ( $n=13$ ), Otuzco ( $n=26$ ), Puno ( $n=69$ ), Santiago de Chuco ( $n=21$ ), and Tupe ( $n=17$ ). The lowlands sample includes individuals from Picota ( $n=21$ ), Picota-Centro ( $n=22$ ), and San Juan del Oro ( $n=60$ ). All population samples were rural indigenous communities with the exception of Ancash, which is comprised of recent local rural migrants to the cities of Huaraz, Chancay, and Lima, or from the small town of Yungay in the *Región* of Ancash. Inclusion criteria included unrelated individuals over 18 years of age with all four grandparents from the designated sample area.

To conduct our tests, we (1) sequenced the mtDNA first hypervariable region (HVI) and determined the mtDNA haplogroup of 611 individuals, and (2) typed 10 Y-STRs and determined the Y-chromosome haplogroup of 272 males. These data were combined with published data for an additional 374 individuals distributed throughout 15 populations in the Peruvian Central Andes (Table 1 and

Figure 1). A comparative sample of 366 individuals from 10 populations from the Amazon and Orinoco River Basin regions (henceforth also designated as “eastern”) was compiled from published sources and a set of unpublished GenBank sequences (Table 2 and Figure 1).

**Laboratory methods.** Each laboratory conducted DNA extractions on a subset of the total sample using a standard phenol/chloroform method (Green and Sambrook 2012). MtDNA haplogroup assignments were conducted at UNMSM and URP on non-overlapping population samples. MtDNA sequencing of all population samples took place at UNM/ASU, and Y-haplogroup assignments and STR fragment analysis took place at ASU.

*MtDNA.* The mtDNA first hypervariable region (HVI) was amplified using one of four PCR primer sets: L15996 and H16401 (Vigilant et al. 1989), L15926 (Kocher et al. 1989) and H16498 (DiRienzo and Wilson 1991), L16055 and H16410 (Handt et al. 1996), or L15936 (5'-CTTGTAACCGGAGATGAAA-3') and H16498 (DiRienzo and Wilson 1991). PCR products were purified using shrimp alkaline phosphatase (Affymetrix/USB) and Exonuclease I (Affymetrix/USB), and sequenced in forward and reverse directions using the BigDye protocol (Applied Biosystems) on an Applied Biosystems 3730 capillary sequencer.

We typed four major Native American founder haplogroups (A-D) through the identification of diagnostic HVI polymorphisms. Haplogroup assignments were verified through PCR amplification of characteristic mtDNA markers, followed by restriction enzyme typing (*Hae*III, *Hinc*II, or *Alu*I) or by the presence/absence of the COII/tRNA<sup>Lys</sup> 9 base-pair deletion, as described previously (Stone and Stoneking 1998). When mtDNA sequences were not diagnostic of one of four major Native American haplogroups (A-D), we sequenced additional sections of the mtDNA coding region using primers in Ramos et al. (2009; Table 1, primer sets 2, 8, and 9). Haplogroups for these samples were defined using Phylotree<sub>mt</sub> (mtDNA tree build 16; Date: 19 Feb 2014; van Oven and Kayser 2009).

*Y-chromosome.* Samples were typed for ten Y-STRs: DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, and DYS439 using the Powerplex Y kit (Promega). DYS388 and DYS426 were typed using primers and PCR conditions from Kayser et al. (1997) and Jobling et al. (1997), respectively. STR fragment analysis was conducted either on an ABI 377 gel sequencer or an Applied Biosystems 3730 capillary sequencer and processed using Applied Biosystem's GeneScan® and Genotyper® software.

All samples were initially screened for M242, M3, and M19 SNPs that are diagnostic of Y-haplogroups Q\*, Q1a2a1a1, and Q1a2a1a1a, respectively. Any

sample within the Q\* paragroup was subsequently typed for the M346 SNP that is diagnostic of haplogroup Q1a2. If a sample did not fall into Y chromosomal haplogroup Q, haplogroups were predicted via a Bayesian approach (Athey 2006) implemented in the Haplogroup Predictor web interface ([www.hprg.com/hapest5](http://www.hprg.com/hapest5)). Haplogroup predictions were verified through direct sequencing of diagnostic SNPs. All SNP primer sets were derived from Karafet et al. (2008) with the exception of M242, M3, M415, and M420. M242 was PCR-amplified using the primer set 5'-CCTTGCTGTCTAGTTCCTAG-3' and 5'-AATACCTTACCTAGAACAACCTC-3', and typed using the *BsiHKA*I restriction enzyme (New England BioLabs). M3 was amplified using mismatch primers from Santos et al. (1999) and typed using the *Mfe*I restriction enzyme (New England BioLabs). Primer sets for M415 and M420 are from Myers et al. (2011) and Hinds et al. (2005), respectively.

**Analytical methods.** Analyses of mtDNA and Y-chromosome variation of traditional populations in the Peruvian Central Andes were limited to Native American founder lineages. Y-chromosome lineages use a notation of lineage-based name followed by the diagnostic SNP (e.g., "Q1a2a1a1-M3"). Y-haplogroup designations are based on the International Society of Genetic Genealogy (ISOGG) 2014 Y-DNA Haplogroup Tree (Version 9.7; Date: 2 June 2014).

MtDNA sequences were aligned to the revised Cambridge Reference Sequence (rCRS; Andrews et al. 1999) and edited using SeqMan Pro (DNASTAR Lasergene 11). We excluded nucleotide positions (np) 16182 and 16183 because these positions are dependent on the presence of a C mutation at np 16189 (Pfeiffer et al. 1999). Analyses also excluded any cytosine inserts between np 16193-16194, as these may be present due to individual sequence length heteroplasmy (c.f., Irwin et al. 2009) or to differences in sequencing methods among labs. To facilitate comparisons with other published data sets, we cropped all mtDNA HVI sequences from np 16084 to 16364 and limited our Y-chromosome analyses to six STRs (DYS19, DYS389I, DYS389B, DYS390, DYS391, DYS393) within Q1a2a1a1-M3. DYS389B was calculated by subtracting DYS389I from DYS389II. Additionally, Y-chromosomes from three eastern population samples (Gavião, Suruí, Zoró) were combined into a single sample to replicate the analysis in Tarazona-Santos et al. (2001); however, we found that our results were robust when compared to alternative groupings, such as Gavião only, Gavião with either Suruí or Zoró, or all three separately.

To test the hypothesis that populations throughout the Peruvian Central Andes contain patterns of high within- and low-between population genetic diversity, we assessed distributions of population diversity by estimating average gene diversity within mtDNA HVI and Y-STR haplotypes ( $\pi$  and  $D$  estimates, respectively; Nei 1987). We further assessed levels of population genetic



differentiation within ecozones through the estimation of  $\phi_{st}$  between pairs of populations (Excoffier et al. 1992). Because previous claims of “high” within- and “low” between-population variation in the Peruvian Central Andes are based on a comparison to the same or similar measures in eastern South American populations, we conducted analyses on available population samples from the Amazon and Orinoco River Basins (see Table 2). Furthermore, because previous analyses focused exclusively on highland populations, we also conduct these tests using only Peruvian highland samples versus eastern samples. These estimates were generated using Arlequin v.3.5.1.3 (Excoffier and Lischer 2010).

Nonparametric randomization tests in which the observed difference in average  $\pi$  or  $D$  estimates of populations within regions (“west” or “east”) was compared to a distribution of estimates obtained from 5,000 random permutations of the original data with replacement; these were executed in Microsoft Excel v.14.4.3.

To ascertain the extent to which events from the last millennium could account for extant genetic structure in the Peruvian Central Andes, we (a) explored relative patterns of the apportionment of variation among populations in different ecozones using analyses of molecular variance (AMOVA; Excoffier et al. 1992). We also (b) investigated potential effects of sex biased gene flow on patterns of genetic variation in two ways: We first assessed correlations between genetic and geographic distances using Mantel tests (Mantel 1967; Smouse et al. 1986) using PASSaGE 2 (Rosenberg and Anderson 2011). Mantel tests were

statistically evaluated using Bonferroni-corrected probabilities. For mtDNA,  $\phi_{st}$  genetic distances were estimated using the Tamura-Nei evolutionary model (Tamura and Nei 1993) with the gamma distribution parameter alpha ( $\alpha$ ) set at 0.26 (Meyer et al. 1999). For Y-STRs, distances were estimated using a stepwise mutation evolutionary model ( $R_{st}$ ; Slatkin 1995). Genetic distance analyses were performed using Arlequin v.3.5.1.3 (Excoffier and Lischer 2010). Great circle geographic distances were calculated using the longitude and latitude coordinates for each sample site using PASSaGE 2. Second, we assessed differences in the genetic structure of males and females using the parameter  $Nv$ , calculated as  $(1/\phi_{st}) - 1$  (Cavalli-Sforza and Bodmer 1971). Different  $Nv$  values between the two genetic systems reflect differences in migration rates and/or effective population sizes, as mutation rate may be considered negligible (c.f., Destro-Bisol et al. 2004; Bolnick et al. 2006).

Last, to visualize patterns captured by the above analyses, we used principal coordinate (PCO) plots using  $\phi_{st}$  and  $R_{st}$  genetic distances, as above. PCO analyses were carried out using QIIME Pipeline python scripts (Caporaso et al. 2010) and visualized using KiNG v.2.21 (Chen et al. 2009).

## **Results**

### **Mitochondrial DNA and Y-chromosome haplogroup/haplotype distributions.**

*MtDNA.* The vast majority (99.3%) of individuals in the study sample belonged to Native American founder haplogroups A-D (Table 3). Three population samples (Huancapi, Picota, and Picota Centro) exhibited a 100% frequency of Haplogroup B, and several others contained high frequencies of Haplogroup B, such as Cara Cara (96%) and Cusco-North (78%). The rest of the population samples contained varying proportions of lineages A-D. Four individuals exhibited non-founder mtDNA lineages, specifically, African mtDNA haplogroup L haplotypes (Salas et al. 2004; Behar et al. 2008; van Oven and Kayser 2009; Soares et al. 2012) and likely represent recent (post-A.D. 1492) admixture. These four individuals were distributed in three population samples (Andahuaylas, Catacaos, and Caleta Santa Rosa; Appendix 1).

We additionally identified a geographically uneven distribution of a single mtDNA haplotype (16189C, 16217C, 16242T, and 16324C) among our sampled populations (and in one published sample, the Tayajaca; see Table 4). Several of the lowland samples demonstrated either a 100% (Picota and Picota Centro) or a very high percentage (e.g., San Juan del Oro, 43%) of this haplotype, and one of our highland samples (Huancapi) also demonstrated 100% of this haplotype, while another (Cara Cara) was at 96%.

*Y-chromosome.* Sixteen biallelic polymorphisms on the Y-chromosome were characterized in nine population samples, resulting in 12 Y-chromosome haplogroup lineages (Appendix 2). Approximately 92% of males characterized exhibited one of two Native American founder haplogroups: Q1a2-M346, comprising 1.4% of the total sample, and Q1a2a1a1-M3, comprising 90% of the total sample. Other, presumably non-founder, Y haplogroups consisted of R1b1-M415 (9.2%), E-M96 (1.1%), J-M304 (2.6%), G-M201 (1.8%), R1b-M343 (0.7%), I-M170 (0.7%), and R1a1-SRY<sub>10831.2</sub> (0.4%). Many of these non-founder haplogroups were distributed within the Ancash sample, followed by the Andahuaylas sample, and then were sparingly present in the rest of the samples, except for Picota and Picota-Centro, which contain none (Appendix 2). We additionally screened R1b-M415 samples for R1b1a1-M73 (Malyarchuk et al. 2011) to investigate the possibility that these R1b lineages, typically attributed to European male admixture, might instead be of Asian origin (Bortolini et al. 2003; Kemp and Schurr 2010; Lell et al. 2002), but no sample had the diagnostic M73 SNP.

The Q1a2a1a1-M3 “modal haplotype,” 13.10.17.24.10.13, identified in previous Y-chromosome studies among Native South Americans (Bianchi et al. 1998; Tarazona-Santos et al. 2001) was absent in our sample. The most frequent (22%) Q1a2a1a1-M3 haplotype, 13.14.18.23.10.14, occurred mostly in lowland samples (Picota, Picota-Centro, and San Juan del Oro), and furthermore was the

only haplotype found in the Picota and Picota-Centro samples (excluding individuals with missing data).

**Patterns of within- and between-population genetic variation.** Prior characterizations of western Andean population genetic variation assume a strong distinction from eastern South American populations. In our reanalysis, the contrast between “west” and “east” is not as stark as reported previously.

In the case of mtDNA, the relative comparison between “west” and “east” is inconsistent with previous reports (i.e., Fuselli et al. 2003; Cabana et al. 2006). The western Andes shows *lower*, not higher, estimates of within-population diversity. In our study, average within-population  $\pi$  estimates for the entire Peruvian Central Andes and the Peruvian highlands are 0.01861 and 0.0192, respectively, relative to 0.0320 in the eastern region (Table 5). Comparisons of the Peruvian highland and coast with eastern populations are statistically significant at  $p \leq 0.05$ , but the Peruvian lowland-eastern South America comparison is not ( $p = 0.37$ ). In terms of population differentiation, the Peruvian Central Andes as a whole ( $\phi_{st} = 0.1833$ ) and its highland and coastal areas ( $\phi_{st} = 0.1522$  and 0.1170, respectively) have lower estimates than the Amazon/Orinoco River Basins ( $\phi_{st} = 0.2155$ ). In other words, throughout the Peruvian Central Andes, and especially within the highlands, approximately 18% of the variation is apportioned among populations, versus 21% in eastern South America; these

values are not substantially different from one another. The Peruvian lowland ecozone is exceptional, exhibiting relatively high population differentiation estimates ( $\phi_{st} = 0.3189$ ).

A handful of highland populations exhibited low mtDNA diversity levels. For example, Huancapi and Cara Cara demonstrated extraordinarily low diversity estimates ( $\pi = 0$  and 0.0021, respectively) due to their high frequencies of the mtDNA haplogroup B haplotype (16189C, 16217C, 16242T, and 16324C) described above. To date, no other reported highland Andean population sample has exhibited such low mtDNA diversity.

In contrast to the mtDNA results, Peruvian Central Andean Q1a2a1a1-M3 Y-chromosomes exhibited higher, but statistically non-significant, average gene diversity estimates relative to the eastern region ( $D = 0.3803$  vs. 0.3007, respectively;  $p = 0.16$ ) (Table 6); the Peruvian highland area showed a much higher and significant relative value ( $D = 0.4248$ ;  $p = 0.03$ ). Population differentiation was lower in the Peruvian Central Andes overall ( $\phi_{st} = 0.4147$ ), as well as in the highlands ( $\phi_{st} = 0.4042$ ) and lowlands ( $\phi_{st} = 0.2500$ ) compared to the eastern estimate ( $\phi_{st} = 0.6265$ ). This indicates that the eastern region contains about 20% more variation apportioned among populations relative to the Peruvian Central Andes. Interestingly, however, highland population Y-chromosomes were much more differentiated than found previously (Tarazona-Santos et al. 2001; Yang et al. 2010). For example, Tarazona-Santos et al. (2001) report a

pooled Central Andean  $\phi_{st}$  estimate of 0.024, but our comparative analyses demonstrated a much higher estimate for highland populations as well as those within the entire Peruvian Central Andes.

**Population genetic structure by ecozone.** To address the second hypothesis, we first sought to assess the degree to which highland populations were differentially affected by Inca and Spanish policies relative to lowland and coastal populations, if at all. The hypothesis is supported for mtDNA but not for Y-chromosome data. AMOVA analyses for both genetic systems show minimal, often non-significant, differences in the apportionment of variation among ecozones. When within and among population apportionments of variation are analyzed independently for each ecozone, highland groups have higher amounts of within group variation for mtDNA but not for Y-chromosome data (Table 7).

More specifically, mtDNA-based AMOVA analyses of multiple comparisons among ecological zones showed most (~ 67-82%) genetic variation distributed within populations; the little genetic variation that was apportioned among zones rarely reached statistical significance after 10,000 permutations (Table 7). This general lack of structure by ecological zone was apparent in the mtDNA PCO plot depicting the first two principal coordinates (Figure 2A) in which the first and second PCO captured 46% and 24% of the total variance in the data, respectively. Highland, coastal, and lowland samples were intermixed. Four

samples that form a somewhat distant cluster along the first PCO axis – Cara Cara, Huancapi, Picota, and Picota-Centro – all share very high frequencies of the mtDNA haplogroup B haplotype (16189C, 16217C, 16242T, and 16324C) mentioned above. A comparison of the apportionment of variation within and among populations by ecozone shows that a large proportion of genetic variation in coastal and highland zones is found within (~ 85-88%) rather than among (12-15%) populations, while in the lowlands, only 68% was distributed within, and up to 31% among populations.

Y-chromosome-based AMOVA analyses showed genetic variation also as weakly and insignificantly apportioned between highland and lowland ecozones, with a little more than half (~55%) of genetic variation distributed within populations and the rest among populations within ecozones. The Y-chromosome PCO plot visually depicts the general lack of structure between highland and lowland samples (Figure 2B). The first and second PCO captured 47% and 24% of the total variance in the data, with highland and lowland samples for the most part intermixed along both axes, with the exception of two clusters of samples. One cluster, consisting of Cara Cara, Picota, and Picota Centro, shares high frequencies of a single Y haplotype (13.14.18.23.10.14) within Q1a2a1a1-M3. A second cluster, consisting of Tayacaja and Arequipa, shares many haplotypes in common to the exclusion of most or all other Peruvian Central Andean populations. Finally, as pointed out above, much more variation is



apportioned among, versus within, groups in the highlands relative to those in the lowlands.

**Sex-specific patterns of population genetic structure.** A secondary hypothesis related to the potential effect of Inca and Spanish policies was an expected lack of sex bias in the extant pattern of population genetic variation throughout the Peruvian Central Andes, and in the highlands especially. This secondary hypothesis is rejected: though Mantel tests lacked evidence of distance-based patterning of either maternal or paternal genetic variation,  $N_v$  values between the two genetic systems reveal higher female effective sizes and/or gene flow in the Peruvian highlands; the converse is true for the Peruvian lowlands.

Mantel tests yielded low and statistically insignificant correlations between genetic and geographic distances for both genetic systems. For mtDNA, the Mantel statistic was low ( $r = 0.1555$ ) but non-significant at  $p = 0.03$  [critical  $p$ -value = 0.002]. For the Y-chromosome, the Mantel statistic was slightly negative ( $r = -0.5142$ ) and non-significant at  $p = 0.67$  [critical  $p$ -value = 0.003]. Both PCO plots depict this lack of correspondence; while pairs of spatially proximate population samples cluster together somewhat along either the first or second PCO axis, relationships among population samples generally do not readily relate to geographic location (Figure 2).

Maternally and paternally inherited loci showed opposite patterns of genetic differentiation ( $\phi_{st}$ ) among populations (Tables 5 and 6). MtDNA indicates high differentiation in the lowlands ( $\phi_{st} = 0.32$ ), and approximately equal levels in the highlands ( $\phi_{st} = 0.15$ ) and the coast ( $\phi_{st} = 0.12$ ), whereas Y-chromosomes indicate low differentiation in the lowlands ( $\phi_{st} = 0.25$ ) and high differentiation in the highlands ( $\phi_{st} = 0.40$ ). The  $\phi_{st}$  values for the Peruvian Central Andes produce a ratio of mtDNA to Y-chromosome  $Nv$  of 3.05, indicating a female migration rate and/or effective size that is more than three times that of males. In the Peruvian highlands, the ratio is even larger ( $Nv = 3.78$ ), while in the lowlands, it is lower ( $Nv = 0.71$ ), suggesting the male migration rate and/or effective size is almost 1.5 times higher than that of females.

## **Discussion**

This study presents a comprehensive investigation of population genetic variation in the Peruvian Central Andes with the purpose of contributing to the reconstruction of the region's population history. To this end, the study analyzes maternally inherited mtDNA HVI and paternally inherited Y-chromosome STRs of 17 novel population samples combined with 15 published population samples. With this large number of samples covering multiple ecological areas throughout the Peruvian Central Andes, we (1) revisit the long-standing characterization of

Andean population genetic variation as relatively unstructured as compared with eastern South American populations, and (2) assess the extent to which state expansion and colonialism during the last half millennium might have (a) differentially affected highland communities and/or (b) generated a lack of sex bias in population genetic structure.

As noted in the introductory section, an overall pattern of high- within and low-between population variation in the Andes relative to eastern South America has been a consistent finding across multiple genetic-based studies. Our results reject a *consistent* pattern of relatively high-within and low-between population variation for both genetic systems. For the Peruvian Central Andes, mtDNA HVI within-population diversities were low, rather than high, relative to values for eastern populations, and only highland Y-chromosomes exhibited significantly higher within-population diversities compared to eastern Y-chromosomes. Also in contrast to previous studies, we found several population samples within the Peruvian highlands as well as throughout the Peruvian Central Andes with relatively low mtDNA genetic diversity estimates. These results are partly due to the fact that the characterization of eastern population structure differs from previous reports due to our inclusion of novel samples. Eastern population diversities for both genetic systems are higher, and eastern Y-chromosomes are twice as differentiated than previously reported (Tarazona-Santos et al. 2001; Fuselli et al. 2003; Cabana et al. 2006).

Up until this point, the characterization of a relative lack of population genetic structure in the Andean region versus eastern South America has gone unchallenged. Instead, recent work has built on the presumed weak structure to argue against a dual founder model for the peopling of South America (Lewis and Long 2008; Lewis 2009), and to argue for the possibility of range expansion by a single founding population into the Central Andes (Yang et al. 2010; Batai and Williams 2014). However, by simply increasing the number and geographical coverage of populations sampled, we show that populations on either side of the Andean range do not have contrasting – or even opposing – patterns of genetic variation, and thus cannot be easily characterized as two distinct “meta” (Lanata and García 2005) or “mega” (Pucciarelli et al. 2006) populations. This is the case even if we confine our definition of “western Andes” to highland regions only.

Explanations for the presumed dichotomous pattern have focused on migratory events in early South American prehistory, presumably because large-scale migrations of distinct founder populations could reasonably explain why such clear and distinctly opposing patterns of population structure were observed over such large, well-defined geographic areas several millennia later. The fact that this explanation has dominated discussions, however, means that the role of other or additional (pre)historical phenomena in shaping extant patterns of population genetic variation in the Andes has been underexplored. In order to forward that exploration, we chose to focus on the Inca imperial and Spanish

colonial policies from the last half millennium because (1) they are recent phenomena relative to the region's ca. 15,000 years of prehistory (Dillehay 2009), and (2) they generate clear expectations of the structure of population genetic diversity.

Thus, our second hypothesis investigates population structure solely within the Peruvian Central Andean region, by ecozone and/or by genetic system. Archaeological and ethnohistorical accounts led us to expect weak signals of population genetic structure and a lack of sex bias in gene flow and/or effective size estimates, particularly in the Peruvian highlands relative to the coast and lowlands. Our results show that Peruvian highland communities do exhibit weak population genetic structure relative to other ecozones only for mtDNA, and not for Y-chromosome, data. Second, highland populations exhibit higher levels of female- vs. male-mediated gene flow and/or high effective sizes relative to other regions, while the lowlands show the opposite pattern. Though our results provide strong evidence for high levels of gene flow and/or effective sizes among *females* in Peruvian highland groups, they do not fully support our expectations for both genetic systems. These results therefore provide – at best – equivocal evidence for a strong influence of combined Inca and Spanish policies on population genetic variation throughout the Andes or in highland regions only.

Population genetic structure in the Andes does not appear to be dictated by large-scale phenomena and may instead be understood via an exploration of more

spatiotemporally defined processes. Archaeological, ethnohistorical, and recent paleogenetic studies of the Central Andes encourage a finer-grained analysis. These studies show early geographic and diachronic variation in the area: from the time of initial colonization, hunter-gatherers engaged in diverse subsistence practices with varying patterns of mobility, including sedentism, transhumance, and long-distance foraging – practices that probably isolated some human populations regionally (e.g., Aldenderfer 2008; Sandweiss 2008). As food production became central to the subsistence economies and social organization of most Andean societies (particularly after 3000 B.C.), groups increasingly engaged in contacts that spread crops, craft goods, and cultural practices within and among regions (Perry et al. 2006; Haas et al. 2013). Andean urban centers emerged around A.D. 400-600, signaling the presence of centralized and hierarchical societies with subsistence strategies favoring rapid population growth rates (Read and LeBlanc 2003). State expansion, in which central political control was exercised over large territories, occurred in multiple locations. In the case of Wari and Tiwanaku, state populations also established colonies. Wari and Tiwanaku disintegrated around A.D. 1000, replaced by agropastoral societies that used broad kin-based networks to access diverse resources. Populations grew markedly across the highlands until ~A.D. 1400, when imperial expansion of the Inca state likely altered the region's demography. Spanish documents indicate that by the mid-sixteenth century, the region displayed diverse ethnic groups,

languages, and dialects (Mannheim 1991). Moreover, paleogenetic studies suggest that local dynamics may have deviated from broader-scale processes over the last 500 years in the Andean region. Studies by Baca et al. (2014), Kemp et al. (2009), and Lewis et al. (2007b) present evidence for spatiotemporal continuity of populations, while Fehren-Schmitz et al. (2011) find evidence for both continuity and discontinuity of populations that differ between maternally and paternally inherited loci. Notably, our study's identification of an uneven geographic distribution of a single mtDNA B haplotype hints at localized instances of gene flow and drift.

## **Conclusions**

Over the last two decades, studies of continent level population genetic variation and structure have been executed under the presumption that either a single or dual founder colonization model would best explain observed patterns. Our study upends this research trend by rejecting the presumed dichotomous pattern of South American population genetic structure.

Importantly, our study contributes greater nuance to the “western” pattern. We have shown that with denser population and genomic-level sampling, the “west” reveals finer-scale patterns of population genetic variation than formerly recognized. These patterns may result from relatively localized and historically

contingent processes, rather than from single major trends or causal variables. We suggest that future endeavors in the Peruvian Central Andes strive for denser geographic and genomic coverage using both ancient and modern DNA techniques to better access local (pre)histories at multiple spatial and temporal scales.

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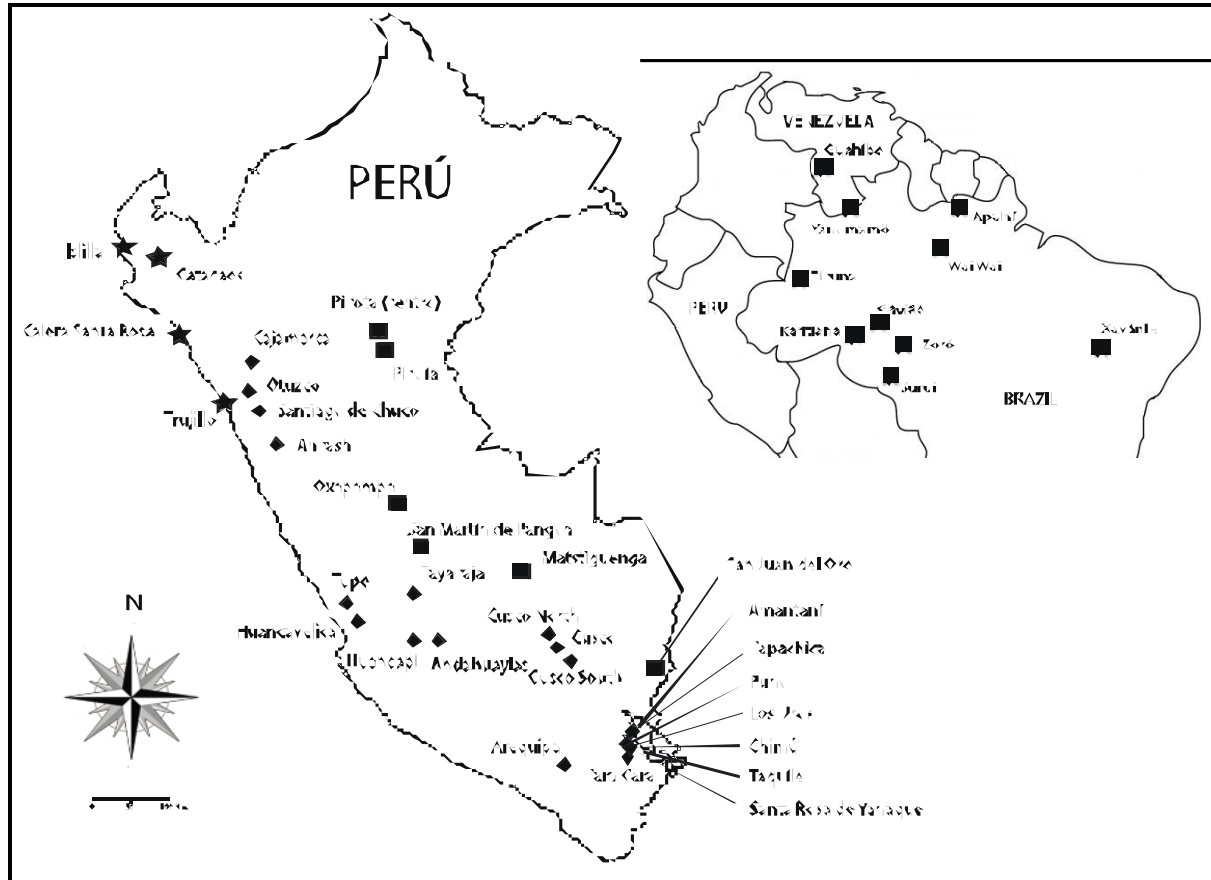
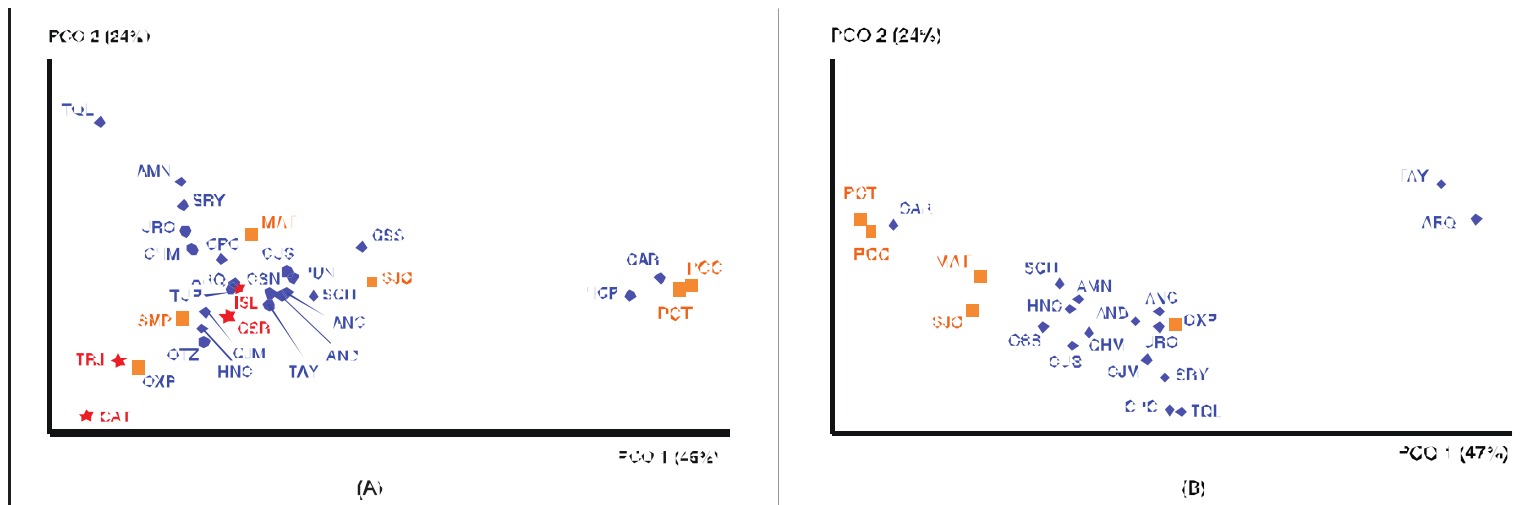


Figure 1. Map of Perú and eastern South America with sampling locations. For the Peruvian Central Andes, coastal samples are designated with stars, highland samples with circles, and lowland samples with squares. Eastern samples from the Amazon and Orinoco River Basins are designated with Xs.





**Figure 2.** First two principal coordinates based on (A) mtDNA HVI pairwise  $\phi_{st}$  and (B) Y-haplogroup Q1a2a1a1-M3 pairwise  $R_{st}$  distance estimates. Axes are labeled with the percentage of variance explained. Coastal population samples are designated with stars, highland samples with circles, and lowland samples with squares. Populations and their abbreviations are: Amantani (AMT), Ancash (ANC), Andahuaylas (AND), Arequipa (ARQ), Cajamarca (CJM), Caleta Santa Rosa (CSR), Capachica (CPC), Cara Cara (CAR), Catacaos (CAT), Chimú (CHM), Cusco (CUS), Cusco North (CSN), Cusco South (CSS), Huancapi (HCP), Huancavelica (HNC), Isilla (ISL), Los Uros (URO), Matsiguenga (MAT), Otuzco (OTZ), Oxapampa (OXP), Picota (PCT), Picota Centro (PCC), Puno (PUN), San Juan del Oro (SJO), San Martín de Pangoa (SMP), Santiago de Chuco (SCH), Taquile (TQL), Tayacaja (TAY), Trujillo (TRJ), Tupe (TUP).

**Table 1.** Peruvian Central Andean Populations: Sample Locations and Data Sources

<i>Population sample name</i>	<i>Región</i>	<i>Geographic coordinates</i>		<i>mtDNA</i>		<i>Y-chromosome</i>	
		<i>Latitude</i>	<i>Longitude</i>	<i>Reference</i>	<i>n</i>	<i>Reference</i>	<i>n</i>
Amantani	Puno	-15.67	-69.71	Sandoval et al. 2013	26	Sandoval et al. 2013	26
Ancash	Ancash	-9.33	-77.56	Lewis et al. 2004; Lewis et al. 2007	73	This study	41
Andahuaylas	Apurimac	-13.66	-73.38	This study	56	This study	35
Arequipa	Arequipa	-13.13	-71.11	Fuselli et al. 2003	22	Tarazona-Santos et al. 2001	15
Cajamarca	Cajamarca	-7.16	-78.51	Sandoval et al. 2013	19	Sandoval et al. 2013	19
Caleta Santa Rosa	Lambayeque	-7.13	-79.55	This study	31	---	-
Capachica	Puno	-15.67	-69.85	Sandoval et al. 2013	15	Sandoval et al. 2013	15
Cara Cara	Cusco	-15.48	-70.35	This study	26	This study	28
Catacaos	Piura	-5.27	-80.68	This study	16	---	-
Chimú	Puno	-15.86	-69.95	Sandoval et al. 2013	16	Sandoval et al. 2013	16
Cusco	Cusco	-13.52	-71.97	Sandoval et al. 2013	36	Sandoval et al. 2013	36
Cusco-North	Cusco	-13.52	-71.98	This study	34	This study	54
Cusco-South	Cusco	-14.6	-71.25	This study	95	---	-
Huancapi	Ayacucho	-13.66	-74.05	This study	13	---	-
Huancavelica	Huancavelica	-12.93	-75.15	Sandoval et al. 2013	26	Sandoval et al. 2013	26
Islilla	Lambayeque	-5.12	-81.11	This study	18	---	-
Los Uros	Puno	-15.74	-69.93	Sandoval et al. 2013	25	Sandoval et al. 2013	25
Matsiguenga	Cusco	-12	-72.30	Mazières et al. 2008	38	Mazières et al. 2008	13
Otuzco	La Libertad	-7.91	-78.56	This study	26	---	-
Oxapampa	Pasco	-10.59	-75.40	Sandoval et al. 2013	18	Sandoval et al. 2013	18
Picota	San Martín	-8.2	-75.98	This study	21	This study	21
Picota-Centro	San Martín	-6.92	-76.33	This study	22	This study	22
Puno	Cusco	-15.84	-70.02	This study	69	---	-
San Juan del Oro	Cusco	-14.12	-69.12	This study	60	This study	56
San Martín de Pangoa	Junín	-11.43	-74.48	Fuselli et al. 2003	17	---	-
Santa Rosa de Yanaque	Puno	-15.95	-69.67	Sandoval et al. 2013	18	Sandoval et al. 2013	18
Santiago de Chuco	La Libertad	-8.15	-78.18	This study	21	This study	13
Taquile	Puno	-15.77	-69.68	Sandoval et al. 2013	35	Sandoval et al. 2013	35
Tayacaja	Tayacaja	-12.24	-74.34	Fuselli et al. 2003	63	Tarazona-Santos et al. 2001	44
Trujillo	La Libertad	-8.11	-79.03	This study	13	---	-
Tupe	Lima	-12.74	-75.81	This study	17	---	-

**Table 2.** Amazon and Orinoco River Basin Populations: Sample Information and Data Sources

<i>Population sample name</i>	<i>mtDNA HVI</i>		<i>Y-chromosome Q1a2a1a1-M3</i>	
	<i>Reference</i>	<i>n</i>	<i>Reference</i>	<i>n</i>
Gavião	Ward et al. 1996	28	Tarazona-Santos et al. 2001	17
Apalaí	Mazières et al. 2008	102	Mazières et al. 2011	28
Guahibo	Vona et al. 2005	59	—	—
Karitiana	Zheng et al. n.d.	24	Tarazona-Santos et al. 2001	8
Suruí	Fuselli et al. 2003	22	Tarazona-Santos et al. 2001	5
Ticuna	Yang et al. 2010	12	Tarazona-Santos et al. 2001	32
Wai Wai	Bonato and Salzano 1997	25	Tarazona-Santos et al. 2001	5
Xavánte	Bonato and Salzano 1997	25	Tarazona-Santos et al. 2001	5
Yanomamö	Hunley et al. 2008	40	—	—
Zoró	Ward et al. 1996	29	Tarazona-Santos et al. 2001	4

**Table 3.** MtDNA and Y-Chromosome Native American Founder Haplogroup Counts (Frequencies) in Peruvian Central Andean Population Samples

<i>Population sample</i>	<i>mtDNA haplogroup</i>				<i>n</i>	<i>Y-chromosome haplogroup</i>			<i>n</i>
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>		<i>Q</i> *-	<i>Q1a2</i> -	<i>Q1a2a1a1</i> -	
						<i>M242</i> <sup>⌘</sup>	<i>M346</i> <sup>⌘</sup>	<i>M3</i>	
Ancash	5 (.069)	35 (.486)	18 (.25)	15 (.205)	73	2 (.08)	2 (.08)	23 (.92)	25
Andahuaylas	9 (.164)	28 (.509)	13 (.236)	5 (.091)	55	2 (.09)	2 (.09)	20 (.9)	22
Caleta Santa Rosa	3 (.08)	12 (.414)	7 (.241)	7 (.241)	29				
Cara Cara		25 (.962)		1 (.038)	26			28 (1)	28
Catacaos	8 (.533)	1 (.067)	5 (.333)	1 (.067)	15				
Cusco-North	3 (.088)	22 (.647)	6 (.176)	3 (.088)	34				
Cusco-South	2 (.021)	74 (.779)	12 (.126)	7 (.074)	95	1 (.021)	1 (.021)	42 (.875)	48
Huancapi		13 (1)			13				
Islilla	3 (.167)	12 (.067)	1 (.056)	2 (.111)	18				
Otuzco	4 (.154)	5 (.192)	8 (.308)	9 (.346)	26				
Picota		21 (1)			21			21 (1)	21
Picota-Centro		22 (1)			22			22 (1)	22
Puno	2 (.029)	46 (.667)	15 (.217)	6 (.087)	69				
San Juan del Oro	14 (.233)	34 (.567)	6 (.1)	6 (.1)	60			55 (1)	55
Santiago de Chuco	2 (.095)	12 (.571)	3 (.143)	4 (.190)	21			10 (1)	10
Trujillo		3 (.231)	3 (.231)	7 (.538)	13				
Tupe		11 (.647)	6 (.353)		17				

<sup>⌘</sup> Note that individuals with the Q1a2-M346 SNP also share the Q\*-M242 SNP, as per Bailliet et al. 2009.

**Table 4.** Distribution of mtDNA B Haplotype (16189C, 16217C, 16242T, 16324C) in the Peruvian Central Andes

<i>Population sample</i>	<i>Ecological zone</i>	<i>n</i>	<i>Haplotype count</i>	<i>Haplotype frequency</i>
Ancash	Highlands	68	1	0.015
Cara Cara	Highlands	26	25	0.962
Cusco-South	Highlands	95	14	0.147
Huancapi	Highlands	13	13	1.000
Otuzco	Highlands	26	1	0.038
Picota	Lowlands	21	21	1.000
Picota-Centro	Lowlands	22	22	1.000
San Juan del Oro	Lowlands	60	26	0.433
Santiago de Chuco	Highlands	21	5	0.238
Tayacaja	Highlands	63	1	0.016

**Table 5.** MtDNA (Haplogroups A-D) HVI Summary Statistics

<i>Population sample</i>	<i>n</i>	<i>No. haplotypes</i>	<i>Nucleotide diversity (<math>\pi</math>)</i>		$\Phi_{st}$
			<i>Within population</i>	<i>Average within population within ecogeographic region</i>	
<i>Peruvian Central Andes</i>				<i>0.01861</i>	<i>0.1883</i>
<i>Highlands</i>			<i>730</i>	<i>0.0192</i>	<i>0.1522</i>
Amantani	26	8	0.0098		
Ancash	73	37	0.0247		
Andahuaylas	55	35	0.0258		
Arequipa	22	17	0.0205		
Cajamarca	19	14	0.0249		
Capachica	15	11	0.0219		
Cara Cara	26	2	0.0021		
Chimú	16	8	0.0183		
Cusco	36	24	0.0250		
Cusco-North	34	26	0.0260		
Cusco-South	95	35	0.0197		
Huancapi	13	1	0.0000		
Huancavelica	26	16	0.0264		
Los Uros	25	5	0.0147		
Otuzco	26	19	0.0281		
Puno	69	41	0.0212		
Santa Rosa de Yanaque	18	10	0.0131		
Santiago de Chuco	21	10	0.0248		
Taquile	35	4	0.0036		
Tayacaja	63	39	0.0266		
Tupe	17	9	0.0250		
<i>Lowlands</i>			<i>176</i>	<i>0.0134</i>	<i>0.3189</i>
Matsiguenga	38	9	0.0092		
Oxapampa	18	7	0.0227		
Picota	21	1	0.0000		
Picota-Centro	22	1	0.0000		
San Juan del Oro	60	13	0.0259		
San Martín de Pangoa	17	10	0.0226		
<i>Coast</i>			<i>75</i>	<i>0.0236</i>	<i>0.1170</i>
Caleta Santa Rosa	29	20	0.0259		
Catacaos	15	7	0.0213		
Islilla	18	10	0.0249		
Trujillo	13	11	0.0223		
<i>Amazon &amp; Orinoco River Basins</i>				<i>0.0320</i>	<i>0.2115</i>
Apalaí	102	16	0.0253		
Gavião	28	7	0.1813		
Guahibo	59	12	0.0179		
Karitiana	24	4	0.0055		
Suruí	22	3	0.0037		
Ticuna	12	4	0.0149		
Wai Wai	25	8	0.0221		
Xavánte	25	4	0.0108		
Yanomamö	40	17	0.0204		
Zoró	29	8	0.0179		

**Table 6.** Y-Chromosome Q1a2a1a1-M3 Summary Statistics

<i>Population sample</i>	<i>n</i>	<i>No. haplotypes</i>	<i>Average gene diversity among loci (D)</i>		<i>Φ<sub>st</sub></i>
			<i>Within population</i>	<i>Average within population within ecogeographic region</i>	
<i>Peruvian Central Andes</i>				<i>0.3803</i>	<i>0.4147</i>
<i>Highlands</i>			<i>395</i>	<i>0.4248</i>	<i>0.4042</i>
	Amantani	26	12	0.4892	
	Ancash	25	12	0.3603	
	Andahuaylas	22	15	0.4658	
	Arequipa	15	10	0.4778	
	Cajamarca	19	14	0.5136	
	Capachica	15	7	0.5063	
	Cara Cara	28	11	0.0688	
	Chimú	16	11	0.5319	
	Cusco	36	18	0.4598	
	Cusco-South	43	25	0.4058	
	Huancavelica	26	17	0.4010	
	Los Uros	25	7	0.3978	
	Santiago de Chuco	10	7	0.4474	
	Oxapampa	18	8	0.4455	
	Santa Rosa de Yanaque	18	12	0.4553	
	Taquile	35	8	0.2927	
	Tayacaja	44	32	0.5021	
<i>Lowlands</i>			<i>129</i>	<i>0.2291</i>	<i>0.2500</i>
	Matsiguenga*	13	6	0.3077	
	Oxapampa	18	8	0.4455	
	Picota*	21	3	0.0151	
	Picota Centro*	22	6	0.0000	
	San Juan del Oro	55	13	0.3771	
<i>Amazon &amp; Orinoco River Basins</i>			<i>50</i>	<i>0.3007</i>	<i>0.6265</i>
	Apalaí	28	8	0.4281	
	Gavião-Suruí-Zoró	26	11	0.3533	
	Karitiana	8	2	0.0417	
	Ticuna	32	9	0.3145	
	Wai Wai	5	3	0.3667	
	Xavánte	5	3	0.3000	

\* Includes haplotypes with missing data.

**Table 7.** Analyses of Molecular Variance (AMOVA)

<i>Genetic locus</i>	<i>Region/sub-region</i>	<i>Ecozone comparison</i>	<i>Percentage of variation</i>		
			<i>Among groups</i>	<i>Among populations within groups</i>	<i>Within populations</i>
mtDNA HVI	<i>Peruvian Central Andes</i>	Coast-Highlands-Lowlands	3.62	16.89	79.49
		Coast-Highlands	4.32*	14.27	81.41
		Highlands-Lowlands	2.59*	17.53	79.88
		Coast-Lowlands	9.67*	22.98	67.35
	<i>Peruvian Central Andes</i>			18.33	81.17
	Highlands			15.22	84.78
	Lowlands			31.89	68.11
	Coast			11.70	88.3
	<i>Amazon &amp; Orinoco River Basins</i>			21.15	78.85
	Y-chromosome Q1a2a1a1-M3	<i>Peruvian Central Andes</i>	Highlands-Lowlands	8.29*	36.19
<i>Peruvian Central Andes</i>				41.47	58.53
Highlands				40.42	59.58
Lowlands				25.00	75.00
<i>Amazon &amp; Orinoco River Basins</i>				37.35	62.65

\*  $P < 0.05$  after 10,000 permutations.



*Appendices* Complete population-level data for both mtDNA HVI and Y-chromosome STRs in Appendix 1 and 2, respectively. [Appendix 1](#) provides mtDNA haplogroup and full (uncropped) sequence data along with four tables summarizing sequence variants by founder haplogroups A-D. Appendix 2 provides Y-chromosome haplogroup and haplotype profiles based on 10 STRs. MtDNA HVI sequences are also deposited in GenBank (GenBank: [numbers here]).









**Appendix 2.** Y-chromosome Haplogroup and Haplotype Data in Nine population Samples from the Peruvian Central Andes<sup>1</sup>

Population Sample	Lab Sample Number	Derived Haplogroup	STR Allele Sizes									
			19	388	389I	389B	390	391	392	393	426	439
Ancash	PE001	R1b1-M415	14	13	14	16	23	11	13	13	12	12
	PE004	Q1a2a1a1-M3	13	12	13	17	24	10	14	14	12	11
	PE005	Q1a2a1a1-M3	13	12	14	19	24	9	14	13	12	11
	PE006	Q1a2a1a1-M3	13	12	14	17	21	10	14	13	12	13
	PE009	I-M170	15	13	13	15	23	10	11	13	11	13
	PE010	R1b1-M415	14	12	13	16	22	11	13	13	12	11
	PE011	R1b1-M415	14	12	13	17	24	11	13	13	12	12
	PE012	R1b1-M415	14	12	12	17	24	10	13	14	12	12
	PE013	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	13
	PE014	R1b1-M415	14	12	13	16	24	10	13	12	12	12
	PE016	Q1a2-M346	13	12	13	18	24	10	14	14	12	11
	PE017	R1b-M343	14	12	13	16	25	10	13	13	12	12
	PE018	Q1a2a1a1-M3	13	13	13	18	24	10	14	13	12	14
	PE019	J-M304	14	16	13	16	24	10	13	12	11	10
	PE020	Q1a2a1a1-	13	12	13	17	25	10	14	13	12	12

		M3										
	PE027	Q1a2a1a1-M3	13	12	13	18	21	10	14	13	12	12
	PE028	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	14
	PE031	E-M96	13	12	14	17	24	10	11	13	11	12
	PE032	Q1a2a1a1-M3	13	12	12	16	24	10	14	13	12	13
	PE033	R1b1-M415	14	12	14	16	23	10	13	13	12	12
	PE034	R1b1-M415	14	12	12	16	24	10	13	13	12	12
	PE035	R1b1-M415	14	12	14	16	23	11	13	13	12	12
	PE036	R1b1-M415	14	12	13	16	24	11	13	13	12	12
	PE037	R1b1-M415	14	12	13	15	24	10	14	13	13	12
	PE038	Q1a2a1a1-M3	13	12	12	16	24	11	14	13	12	13
	PE040	R1b1-M415	14	12	13	16	24	10	13	13	12	12
	PE075	Q1a2a1a1-M3	13	13	13	18	24	10	14	13	12	12
	PE076	Q1a2-M346	13	12	13	17	24	10	14	12	12	10
	PE078	Q1a2a1a1-M3	14	12	12	17	24	10	14	13	12	14
	PE083	R1b1-M415	14	12	13	16	24	9	16	13	12	13
	PE086	Q1a2a1a1-M3	13	13	13	17	25	10	14	14	12	13
	PE087	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	12
	PE088	Q1a2a1a1-	13	13	13	17	24	10	14	13	12	13

		M3										
	PE090	Q1a2a1a1-M3	13	13	13	18	24	10	14	13	12	13
	PE095	Q1a2a1a1-M3	13	12	13	18	21	10	14	13	12	12
	PE097	Q1a2a1a1-M3	14	12	12	17	24	10	14	13	12	14
	PE099	Q1a2a1a1-M3	13	12	13	18	21	10	14	13	12	12
	PE102	Q1a2a1a1-M3	13	12	13	18	24	10	14	13	12	12
	PE103	Q1a2a1a1-M3	13	12	12	17	23	10	15	13	13	12
	PE105	Q1a2a1a1-M3	13	12	13	18	21	10	14	13	12	12
	PE109	Q1a2a1a1-M3	13	12	13	18	24	10	14	13	12	12
Andahuaylas	PE230	Q1a2a1a1-M3	13	12	13	17	24	10	14	13	12	13
	PE231	R1a1-SRY <sub>10831.2</sub>	16	12	13	17	25	10	11	13	12	10
	PE232	Q1a2a1a1-M3	14	12	12	18	24	11	14	13	12	13
	PE233	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	14
	PE234	Q1a2a1a1-M3	13	12	13	17	21	10	14	14	12	13
	PE235	J-M304	14	16	14	16	22	10	11	12	11	12



	PE236	Q1a2a1a1-M3	13	14	14	16	24	11	14	13	12	12
	PE237	R1b1-M415	14	12	13	16	24	11	13	13	12	12
	PE238	Q1a2a1a1-M3	13	12	14	17	24	10	13	13	12	9
	PE239	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	13
	PE240	R1b1-M415	14	12	14	17	24	10	13	13	12	11
	PE241	R1b1-M415	13	12	14	17	23	11	13	13	12	11
	PE242	R1b1-M415	14	12	13	17	24	9	13	13	12	12
	PE243	Q1a2a1a1-M3	13	12	13	17	23	10	14	13	12	14
	PE244	Q1a2a1a1-M3	13	12	13	19	24	10	14	13	12	11
	PE245	Q1a2a1a1-M3	13	12	10	18	25	10	13	13	12	12
	PE246	R1b1-M415	15	12	12	14	24	11	13	13	12	10
	PE247	E-M96	13	12	13	17	24	10	11	13	11	12
	PE248	Q1a2a1a1-M3	13	12	13	17	24	10	14	14	12	13
	PE249	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	12
	PE250	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	13
	PE251	Q1a2a1a1-M3	13	12	14	16	23	10	14	14	12	11
	PE252	Q1a2a1a1-M3	13	12	14	18	21	10	14	13	12	13

	PE253	R1b1-M415	14	12	13	17	24	11	13	12	12	12
	PE254	I-M170	14	14	12	17	22	10	11	13	11	11
	PE273	Q1a2-M346	13	12	13	17	23	10	14	13	12	14
	PE274	R1b1-M415	14	12	13	17	23	10	13	13	12	11
	PE275	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	13
	PE276	Q1a2-M346	13	12	13	16	23	11	14	13	12	11
	PE277	Q1a2a1a1-M3	13	12	13	16	24	10	14	13	12	11
	PE278	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	?	13
	PE281	Q1a2a1a1-M3	13	12	12	15	24	10	14	13	12	12
	PE284	Q1a2a1a1-M3	13	12	14	16	23	11	16	14	12	13
	PE285	R1b1-M415	16	12	12	17	24	11	13	13	12	12
	PE286	R1b1-M415	14	12	13	16	24	10	12	13	12	12
Cara Cara	PE 519	Q1a2a1a1-M3	?	12	14	32	23	10	16	?	12	13
	PE 520	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 521	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 522	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 523	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13

	PE 524	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 525	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 526	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 527	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 528	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 529	Q1a2a1a1-M3	?	12	14	32	23	?	?	14	12	13
	PE 530	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 532	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 533	Q1a2a1a1-M3	?	12	14	32	20	10	16	14	11	13
	PE 535	Q1a2a1a1-M3	13	12	?	32	?	10	16	14	11	13
	PE 536	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 537	Q1a2a1a1-M3	13	12	14	32	?	10	16	14	11	?
	PE 539	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 540	Q1a2a1a1-M3	13	12	?	?	23	?	?	14	12	11

	PE 541	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 542	Q1a2a1a1-M3	13	12	14	32	23	?	?	15	12	13
	PE 543	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	12	13
	PE 544	Q1a2a1a1-M3	13	12	?	?	20	10	16	14	?	?
	PE 545	Q1a2a1a1-M3	?	12	14	32	23	10	?	14	12	13
	PE 546	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 547	Q1a2a1a1-M3	?	12	14	32	23	10	16	14	11	13
	PE 548	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 549	Q1a2a1a1-M3	13	12	?	32	24	?	16	14	11	13
Cusco-North	PE111	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	14
	PE112	Q1a2a1a1-M3	13	13	13	16	24	10	14	13	12	12
	PE113	J-M304	14	16	14	17	23	10	11	12	11	11
	PE114	Q1a2a1a1-M3	13	12	12	16	24	11	15	13	12	11
	PE115	Q1a2a1a1-M3	13	12	14	16	23	10	15	15	12	13
	PE116	Q1a2a1a1-	13	12	14	16	23	10	16	14	12	12

		M3										
	PE117	Q1a2a1a1-M3	13	12	14	16	23	10	16	14	12	12
	PE118	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	13
	PE119	Q1a2a1a1-M3	13	13	14	18	24	11	13	13	12	11
	PE120	Q1a2a1a1-M3	13	12	13	18	24	10	13	13	12	10
	PE121	Q1a2a1a1-M3	14	13	14	17	25	10	14	13	12	12
	PE122	Q1a2a1a1-M3	13	13	13	16	24	10	14	13	12	13
	PE123	Q1a2a1a1-M3	13	12	14	18	23	10	18	14	12	14
	PE124	Q1a2a1a1-M3	13	12	15	18	23	10	14	13	12	13
	PE125	E-M96	13	12	14	18	23	10	11	14	11	10
	PE126	Q1a2a1a1-M3	13	13	13	16	22	11	14	13	12	11
	PE127	Q1a2a1a1-M3	13	12	14	18	23	11	16	14	12	13
	PE128	J-M304	13	16	14	17	23	10	11	12	11	11
	PE129	Q1a2a1a1-M3	13	12	13	16	23	10	14	13	12	12
	PE130	Q1a2a1a1-M3	13	13	13	16	24	10	14	13	12	13
	PE131	J-M304	13	16	14	17	23	10	11	12	11	11

	PE132	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	13
	PE133	Q1a2-M346	13	12	13	16	25	9	14	13	12	12
	PE134	Q1a2a1a1-M3	13	12	13	16	24	10	14	13	12	12
	PE136	Q1a2a1a1-M3	13	12	14	17	23	10	15	13	12	14
	PE137	Q1a2a1a1-M3	13	12	14	17	23	10	15	14	12	13
	PE138	Q1a2a1a1-M3	13	12	13	18	24	10	13	13	12	13
	PE139	Q1a2a1a1-M3	13	12	14	17	23	10	17	14	12	11
	PE140	Q1a2a1a1-M3	13	12	13	19	24	10	13	13	12	12
	PE141	Q1a2a1a1-M3	14	12	14	17	23	10	17	14	12	13
	PE142	Q1a2a1a1-M3	13	12	14	16	23	10	17	15	12	14
	PE143	Q1a2a1a1-M3	13	12	14	17	23	10	17	15	12	13
	PE144	Q1a2a1a1-M3	13	12	14	17	24	10	17	13	12	12
	PE147	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	13
	PE148	Q1a2a1a1-M3	13	12	12	18	24	10	14	13	12	12
	PE149	Q1a2a1a1-	13	12	14	17	23	10	16	14	13	13

		M3										
	PE150	Q1a2a1a1-M3	13	13	13	17	25	10	14	13	12	12
	PE151	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	14
	PE152	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	12
	PE154	Q1a2a1a1-M3	13	13	14	18	23	10	16	14	12	12
	PE155	Q1a2a1a1-M3	13	13	12	17	25	10	14	13	12	11
	PE156	Q1a2a1a1-M3	13	12	14	17	23	10	16	14	12	14
	PE157	Q1a2a1a1-M3	13	13	13	17	24	10	14	13	12	12
	PE158	R1b1-M415	14	13	13	16	24	10	13	13	12	11
	PE159	Q1a2a1a1-M3	13	13	13	17	23	10	16	14	12	14
	PE160	Q1a2a1a1-M3	13	13	13	18	25	10	13	13	12	12
	PE161	Q1a2a1a1-M3	13	13	14	17	23	10	16	14	12	14
	PE162	R1b1-M415	14	12	13	16	23	10	13	13	12	13
	PE163	R1b1-M415	14	13	13	16	23	11	14	13	12	13
	PE164	G-M201	14/15	13	14	17	22	10	11	13	11	11
	PE166	Q1a2a1a1-M3	14	13	13	18	24	10	14	14	12	12
	PE167	J-M304	14	12	13	16	23	10	12	12	11	11

	PE168	J-M304	15	17	13	18	23	10	10	12	11	11
	PE169	E-M96	14	16	12	17	24	10	10	13	11	12
Otuzco	PE 416	R1a-M420	14	12	13	29	24	11	13	13	11	12
	PE 420	Q1a2a1a1-M3	13	12	13	32	21	10	14	13	12	12
	PE 421	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	12	13
	PE 426	R1b-M343	?	12	?	?	?	?	?	?	12	?
	PE 428	Q1a2a1a1-M3	13	12	?	30	24	?	14	14	11	12
	PE 429	R1b-M343	14	12	13	29	24	11	13	13	12	12
	PE 430	R1b-M343	14	12	13	29	24	11	13	12	12	12
	PE 431	R1b-M343	14	12	13	29	24	11	13	13	12	12
	PE 439	Q1a2a1a1-M3	13	12	14	31	21	10	14	13	12	12
	PE 441	Q1a2a1a1-M3	13	12	13	30	23	10	16	14	12	14
Picota	PE 645	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 646	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 647	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 648	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	?
	PE 649	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13



	PE 650	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 651	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 652	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 653	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 654	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 655	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 656	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 657	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 658	Q1a2a1a1-M3	13	12	14	18	23	10	16	13	12	13
	PE 659	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 660	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 661	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 662	Q1a2a1a1-M3	?	12	14	18	?	10	?	?	12	13
	PE 663	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13

	PE 664	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 665	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
Picota Centro	PE 550	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 551	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 552	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 553	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 554	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 555	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 556	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 557	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 558	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	?
	PE 559	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 560	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 561	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13

	PE 562	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 563	Q1a2a1a1-M3	?	12	14	18	23	10	16	14	12	13
	PE 564	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 565	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE 566	Q1a2a1a1-M3	13	12	?	?	?	?	16	14	12	?
	PE 567	Q1a2a1a1-M3	?	12	14	18	23	10	16	14	12	13
	PE 568	Q1a2a1a1-M3	?	12	14	18	?	10	?	?	12	?
	PE 569	Q1a2a1a1-M3	13	12	14	18	23	?	?	14	12	13
	PE 570	Q1a2a1a1-M3	13	12	?	?	23	10	16	14	12	13
	PE 571	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
Santiago de Chuco	PE 446	G-M201	15	12	12	28	22	?	11	14	11	11
	PE 449	Q1a2a1a1-M3	13	12	13	29	24	10	14	13	11	14
	PE 450	G-M201	15	12	12	29	22	10	11	13	12	11
	PE 451	Q1a2a1a1-M3	13	12	13	30	23	10	15	13	11	12
	PE 452	Q1a2a1a1-	13	12	13	30	24	10	14	13	12	13

		M3										
	PE 453	Q1a2a1a1-M3	13	13	13	32	21	10	14	13	11	11
	PE 454	R1b-M343	14	12	13	29	24	11	13	13	11	11
	PE 455	Q1a2a1a1-M3	13	?	13	33	21	10	14	13	11	12
	PE 457	Q1a2a1a1-M3	13	12	13	28	25	10	14	13	11	11
	PE 458	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 459	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 460	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
	PE 462	Q1a2a1a1-M3	13	12	14	32	23	10	16	14	11	13
San Juan del Oro	PE587	Q1a2a1a1-M3	13	12	13	17	24	10	15	13	12	13
	PE588	Q1a2a1a1-M3	13	12	13	17	24	10	15	13	12	13
	PE589	Q1a2a1a1-M3	13	12	12	19	24	10	15	13	12	12
	PE590	Q1a2a1a1-M3	13	12	12	19	24	10	15	13	12	12
	PE591	Q1a2a1a1-M3	14	12	13	18	23	10	14	13	12	11
	PE592	Q1a2a1a1-M3	14	12	13	18	23	10	14	13	12	11

	PE593	Q1a2-M346	16	12	13	16	25	10	14	13	12	12
	PE594	Q1a2-M346	16	12	13	16	25	10	14	13	12	11
	PE595	E-M96	13	12	13	18	24	11	11	13	11	12
	PE596	E-M96	13	12	13	18	24	11	11	13	11	12
	PE597	Q1a2a1a1-M3	13	12	13	18	24	10	16	14	12	13
	PE598	Q1a2a1a1-M3	13	12	13	18	24	10	16	14	12	13
	PE599	Q1a2a1a1-M3	13	12	13	16	24	10	14	13	12	13
	PE600	Q1a2a1a1-M3	13	12	13	16	24	10	14	13	12	13
	PE601	Q1a2a1a1-M3	14	12	14	16	24	10	14	14	12	12
	PE602	Q1a2a1a1-M3	14	12	14	16	24	10	14	14	12	12
	PE605	Q1a2a1a1-M3	13	12	14	17	24	10	14	13	12	14
	PE606	Q1a2a1a1-M3	13	12	14	17	24	10	14	13	12	14
	PE607	R1b1-M415	14	12	13	17	24	11	13	13	12	12
	PE608	R1b1-M415	14	12	13	17	24	11	13	13	12	12
	PE609	Q1a2a1a1-M3	13	12	15	15	25	10	14	14	12	12
	PE610	Q1a2a1a1-M3	13	12	15	16	25	10	14	14	12	12
	PE611	Q1a2a1a1-M3	13	12	14	19	24	11	14	13	12	12

	PE612	Q1a2a1a1-M3	13	12	14	19	24	11	14	13	12	12
	PE613	Q1a2a1a1-M3	13	12	13	17	23	10	14	13	12	12
	PE614	Q1a2a1a1-M3	13	13	13	17	23	10	14	13	12	12
	PE615	Q1a2a1a1-M3	13	12	13	16	23	11	14	13	12	12
	PE616	R1b1-M415	13	12	13	16	23	11	14	13	12	12
	PE617	G-M201	17	12	12	18	22	9	12	13	12	12
	PE618	G-M201	17	12	12	18	22	9	12	13	11	12
	PE619	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE620	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE621	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE622	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE623	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE624	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE625	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE626	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE627	Q1a2a1a1-	13	12	14	18	23	10	16	14	12	13

		M3										
	PE628	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE629	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE630	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE631	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE632	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE633	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE634	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE635	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE636	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE637	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE638	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE639	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE640	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE641	Q1a2a1a1-	13	12	14	18	23	10	16	14	12	13

		M3										
	PE642	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE643	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
	PE644	Q1a2a1a1-M3	13	12	14	18	23	10	16	14	12	13
<sup>1</sup> "?" Indicates missing data												