Rethinking the Andes–Amazonia Divide

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3.2 Genetic diversity patterns in the Andes and Amazonia

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Reconstructing the human past is a complex multidisciplinary task that only makes sense if independent types of evidence are integrated into a consensual and coherent history.

In scientific historical surveys, genetics can be used to reveal genealogical connections between individuals and populations, to assess their past demography and to trace movements of ancestors through time and space (among other applications). In these historical genetic studies, population dynamics and structure are key aspects for understanding the distribution of the present-day genetic diversity of indigenous South Americans, which was shaped by a complex set of evolutionary events involving ancestral populations.

Historical genetics of Native Americans

Genetic analyses of genotypes (DNA inherited from parents) have been used since the 1980s to reconstruct the (pre)history of Native Americans. Available genetic evidence largely supports a common Asian ancestry of Native Americans and Northeast Asians until the Late Pleistocene, <26,000 BP (Santos et al. 1999; González-José et al. 2008; Bodner et al. 2012; Rasmussen et al. 2015). Only a much more limited data set, however, has been applied to the study of indigenous groups of South America specifically (Tarazona-Santos et al. 2001; Jota et al. 2011; Battaglia et al. 2013). The first Native Americans were likely derived from a population living in Beringia at ~18,000 BP (González-José et al. 2008; Rasmussen et al. 2015), which spread through the entire length of the American continent in perhaps less than 2,000 years, initially along the Pacific coastline (Bodner et al. 2012). At the end of this epic journey, South America was first settled around 14,000 BP (Ruiz-Narváez et al. 2005; Rothhammer and Dillehay 2009; Bodner et al. 2012; Rasmussen et al. 2015). Even though South America was the last continental landmass reached by Homo sapiens, it displayed among the richest diversity
of peoples and cultures worldwide (Salzano and Callegari-Jacques 1988), exemplified by the innumerable indigenous languages spoken in pre-Columbian times (Rodrigues 2005).

Although much effort has been expended on understanding the first peopling of the Americas, the indigenous history of South America still requires many detailed studies to be performed by geneticists, archaeologists, physical anthropologists, linguists and other historical scientists. A common view describes South American Indians as derived from North American groups who arrived through the Isthmus of Panama at the end of the Pleistocene (Rothhammer and Dillehay 2009). However, much debate still centres on the timing of the arrival of the first South Amerindians (Bodner et al. 2012) and the dynamics of subsequent flows of migrants from North America (Ruiz-Narváez et al. 2005). Within South America, the spread of ancestral peoples to colonize various landscapes and biomes, which resulted in many biologically and culturally diverse indigenous groups, has also been extensively discussed (Salzano and Callegari-Jacques 1988). These and many other questions on the origins of Native Americans were raised as soon as the first European chroniclers arrived in the New World, as brilliantly illustrated in the sixteenth-century work of Fray José de Acosta (Acosta 1590).

Pre-Columbian demography and population dynamics of South America

European conquistadors reported divergent demographic scenarios across different regions of the Americas, with modern estimates for the total native population in 1492 ranging from 8.4 to 112.5 million people (Thornton 2005). In almost all published population estimates for pre-Columbian South America, the Andes present much the highest population density, with estimates varying from three to 37 million inhabitants, that is, up to three times more people than all remaining areas of the continent combined (Dobyns 1966; Denevan 1976). (Notwithstanding recent upward revisions of estimates of population size in Amazonia [Chapter 1.1], the contrast in density remains.) The high population density in the central part of the Andes, from southern Colombia to northern Chile, was associated, at the time of first contact with Europeans, with the domains of the Inca empire or Tawantinsuyu, the most complex indigenous society found in South America in the sixteenth century (Denevan 1976; D’Altroy 2015). Currently, in the highlands of the Central Andes there remain abundant speakers of indigenous languages, mainly of the Quechua and Aymara families, notably in Ecuador, Peru and Bolivia (as mapped in Figure 1.2.1, Chapter 1.2), where speakers sum up to about 8.5 million (Howard 2011).

Motivated by earlier historical reports, some genetic studies focused on the likely consequences of demographic differences between Andeans and other populations in South America (Luiselli et al. 2000; Rodríguez-Delfín et al. 2001;
This resulted in a model of how populations evolved during the pre-Columbian settlement of South America (Tarazona-Santos et al. 2001) which predicted that indigenous populations from the Central Andes (Quechua- and Aymara-speakers) and from ‘lowland’ areas should fit two contrasting patterns of genetic drift and gene-flow (see Figure 3.2.1).

In the Central Andes, Quechua- and Aymara speakers displayed greater genetic diversity within each local population group, and a higher gene-flow
(migration of individuals and genes) between such groups. Lowland population groups, particularly in Amazonia and in the Central Brazilian Plateau, by contrast, had less genetic diversity within each group (showing more impact of genetic drift, and low effective population sizes), and there was less gene-flow between groups. (For explanations of all technical terminology from genetics used in this chapter – for example, genetic drift, effective population size, autosomal markers, and so on – see Chapter 1.3.) The genetic pattern of the Central Andes was confirmed in a study using many autosomal markers, which also revealed a large repository of genetic diversity among Quechua-speaking populations (Scliar et al. 2012). Another genomic study (Yang et al. 2010) identified the same divide between Amazonia and the Andes, but the authors suggested that it was caused by an early separation of the source populations during initial settlement of South America. This ancient split is not supported by more recent studies, however (Sandoval, Lacerda et al. 2013; Battaglia et al. 2013; Roewer et al. 2013). Besides, a genomic study using a Bayesian dating method (Scliar et al. 2014) has estimated that the population split between Andean Quechua-speakers and Amazonian Shimaa (Machiguenga, Arawak language family) dates to no earlier than 5300 BP. Although the authors suggest an Andean origin for Shimaa, another likely explanation for this shared ancestry would be that some Andean highlanders have an ancient Amazonian origin.

At the phenotypic level, analyses of the cranial morphology of late pre-Columbian South Amerindians (Pucciarelli et al. 2006; see also Chapter 2.2) have also detected a divide between highland and lowland populations. In fact, the genetic model of population evolution (Tarazona-Santos et al. 2001) also predicts that phenotypes should be more homogeneous throughout the Andes, and quite heterogeneous among Amazonian populations. However, Pucciarelli et al. (2006) found no differences in intra-population diversity between the two regions, likely due to the multifactorial inheritance and quantitative nature of skull shape variation, which may also be subject to selection. Indeed, quantitative variation and trait differentiation have been shown to correlate only weakly with effective population size (Wood et al. 2015).

The particular population dynamics of pre-Columbian South America, as detected in genotypes and phenotypes, have often been attributed to historical and present-day differences between the populations of those areas, in both demography and gene-flow patterns. These genetic differences correlate with cultural aspects, such as the advanced agriculture and social complexity observed in the Central Andes, when compared to lowland groups (Tarazona-Santos et al. 2001). (If that cultural contrast is challenged, as by recent revised thinking on social complexity and demographic scale in Amazonia – see Chapter 1.1 – then the correlation is weakened.) Indeed, population (and language family) expansions have frequently been associated with the spread of first farmers worldwide (Diamond and Bellwood 2003) and in South America (Heggarty and Renfrew 2014b). Genetic studies of indigenous populations worldwide (Gignoux et al. 2011) and in
The high population densities observed in the pre-Columbian Central Andes may have been intensified by the development of an ecologically flexible and thereby mobile agricultural package based on maize (Heggarty and Beresford-Jones 2010). Interestingly, a clear divide has also been identified between strains of maize developed in the Andes and Amazonia, in a genetic study of current indigenous and archaeological maize samples (Freitas and Bustamante 2013). This study suggested an initial introduction and further divergence of maize strains at about 5000 BP in the Andes, and 2000 BP in the Amazonia. Furthermore, a genetic study of a human paternal lineage (a Y-chromosome variant – see Chapter 1.3) originating around 5000 BP in northern Peru indicates a recent secondary human dispersal path from north to south through the Central Andes (Jota et al. 2011), which echoes the spread of maize through the Andean highlands (Vigouroux et al. 2008).

Pre-Columbian Amazonia was home to some large urban complexes (Heckenberger et al. 2003), and here too agriculture was practised by many indigenous groups, including those speaking languages of the Tupí and Arawak families (Clement et al. 2015; see Figure 1.2.1 in Chapter 1.2). However, in the Central Andes farming was remarkably advanced, which supported the emergence of many complex societies and the largest pre-Columbian cities found in South America in the sixteenth century (Lumbreras 1974). The relatively homogeneous cultural landscape found in the Central Andes, where some domestic plants and animals were bred to adapt to high altitude (from 1,000 to 4,200 metres above sea level), may also have been an important factor in the establishment of complex societies here. A hierarchically organized society, with advanced farming technology adapted to a high-altitude landscape along the Central Andes, would be expected to display a high inter-population gene flow and to maintain large effective population sizes. These past dynamics of pre-Columbian peoples would result in cultural homogenization along the Central Andes (when compared to Amazonia), facilitated by the use of the pre-Columbian road networks, known under the Incas as the Qhapaq Ñan, and which totalled c. 23,000 km in the sixteenth century (see Figure 3.2.1 and Lumbreras 2004). In contrast, Amazonia and other lowland biomes of South America present much higher cultural and genetic differentiation between indigenous groups (Tarazona-Santos et al. 2001; Wang et al. 2007; Cabana et al. 2014), where populations tend to remain isolated and to differentiate due to environmental conditions or life-styles more dependent on foraging. Much of the human diversity found in South America can also be explained by a fission-fusion model of indigenous populations (Neel and Salzano 1967), where tribal splits and subsequent isolation and drift could explain observable differences, particularly among Amazonian groups.

As for the big-picture pattern of genetic contrasts across South America, different studies give very contrasting results. A large study with 678 microsatellite
loci found a much larger divergence among native groups in eastern South America than in other indigenous populations worldwide (Wang et al. 2007). In another broad genomic study, Reich et al. (2012) used an admixture graph method (AG) to identify three different groups of indigenous populations in South America: in the Andes, Chaco and eastern South America (Amazonia and the Central Brazilian Plateau). Furthermore, they observed low intra-population diversity and high inter-population divergence among indigenous populations of eastern South America. South-eastern South America, which includes the Chaco, Pampas and Patagonia, was identified by Callegari-Jacques et al. (2011) as a third distinctive component of the population structure in the continent, besides the Andes and Amazonia. In other words, even though results presented by different genetic studies (Callegari-Jacques et al. 2011; Reich et al. 2012; Roewer et al. 2013) do not at all agree on a single divide among South American indigenous groups by broad geographic regions, the populations of the Central Andes do always appear as a clearly distinctive regional group.

Cultural influences on population dynamics and history

As discussed above, pre-Columbian population groups in the Central Andes and Amazonia present contrasting general patterns of gene-flow and effective population sizes, which appear to be associated with environmental and cultural differences between these regions. However, widespread cultural heterogeneity can be observed, particularly in Amazonia, ranging from groups with a lifestyle based entirely on hunting and foraging to horticulturalists and farmers, and from nomadic to semi-sedentary populations. Even in the Central Andes, surrounded by complex farming societies, speakers of Uru languages (Adelaar and Muysken 2004) were still practising a foraging life-style associated with lakes and rivers in the Andean Altiplano until as recently as colonial times (Wachtel 1986; and see Figure 4.1.1 in Chapter 4.1). Indeed, a genetic study (Sandoval, Lacerda et al. 2013) was able to identify that Uru populations (the Uros in Peru, and the Uru-Chipaya and Uru-Poopó groups in Bolivia) are clearly differentiated from neighbouring groups in the Altiplano who speak Quechua and Aymara. This suggests that the ancestors of Uru groups derive from population sources different to those of likely more recent farming groups.

On the Central Brazilian Plateau, on the fringes of the Amazonian rainforest, are many Jê-speaking groups. The Xavante, Kayapó and Panará, for example, although practising some rudimentary agriculture by the time of contact in the twentieth century, lived as typical foragers (Neel et al. 1964). In a seminal publication by Neel and Salzano (1967) based on a study of the Xavante, a fission-fusion model was used to explain a pattern of population dynamics that resulted in groups splitting into endogamous tribes, which may have then evolved in relative independence for a while, or fused with another tribe. This dynamic could
result in a rapid evolution of genes and morphological characters, as evidenced by the Xavante, who show a rapid phenotypic divergence in skull shape when compared to other closely related indigenous groups, probably in response to culture-mediated processes (Hünemeier et al. 2012a).

Among lowland populations, demic expansions (the geographical dispersal of growing populations) were frequently associated with farming-dependent societies in South America, such as speakers of Arawak, Carib and Tupí languages (Diamond and Bellwood 2003; see Figure 1.2.1, in Chapter 1.2). A genetic study of the range expansion of Tupí populations revealed a typical isolation-by-distance pattern, while Jê speakers, who are mainly foragers, dispersed in a non-linear pattern (Ramallo et al. 2013). This agrees with the different population structure outcomes expected between foragers (Jê, etc.) and farmers (Tupí, Arawak, etc.), where the latter will be largely impacted by past demographic expansion and dispersal. The more dependent a population is on foraging, the less its dispersal is accompanied by demographic expansion, and each group tends to differentiate without significant gene-flow.

Although demic fusions appear to be common among tribes of the same ethnic group (Neel and Salzano 1967), different languages and cultural practices would tend to prevent fusion between distinct ethnic groups in Amazonia (Hünemeier et al. 2012a) – although see below and Chapter 3.4 on the linguistic exogamy of the Vaupés region. This could be a major cause for the general differences in population dynamics observed between lowland areas and the Central Andes. However, populations with different levels of dependence on agriculture, heterogeneous social organizations and cultural practices, and who have experienced past fission and fusion events, should present a strikingly complex dynamic of demic evolution, particularly in Amazonia.

A genetic divide between indigenous populations of the Andes and Amazonia

In the Central Andes, settlement was dominated by many overlapping cultures succeeding each other ever since the Late Preceramic period (~4500 BP), exemplified by the ancient sites of Caral and Kotosh in Peru. With the establishment of agriculture-based societies between 4000 and 2000 BP, the highlands came to be dominated by farming, which eventually gave rise to the most complex indigenous societies of South America (Heggarty and Beresford-Jones 2010). In the genetic pattern as currently observed, the peopling of the Central Andes fits a demic diffusion model, as first suggested for the Neolithic transition in Europe (Ammerman and Cavalli-Sforza 1984). In this model, a massive movement of people would be connected with the spread of new technologies (agriculture), eventually assimilating all local forager societies – as may be the case of populations who spoke the now almost ‘extinct’ Uru-languages (Sandoval, Lacerda et al. 2013). Since extensive archaeological data
(Stanish 2001) point to a more likely origin on the Pacific coast for the complex societies later found in the Andean highlands, a demic diffusion of farmers could also explain the assimilation of other former highland forager populations who share a recent (<5000 BP) ancestry with current Amazonians (Scliar et al. 2014).

The pre-Columbian occupation of Amazonia presents a much more complex scenario, with a larger diversity of ethnic groups, cultural practices and languages, associated with higher genetic differentiation between those groups, and relatively lower diversity within each group. Given past fission and fusion events, and heterogeneous demographic outcomes for populations with different levels of farming technology and social structures, the evolutionary dynamics of populations suggests this area has been inhabited by a complex human metapopulation (Morris and Mukherjee 2006), within which many dynamic demes have been constantly changing in size, going extinct and re-colonizing other areas through time and space. Because culture (language, farming, rituals, beliefs, and so on) is so important to how humans adapt to new environments, it may be that density-dependent habitat selection (Fretwell and Lucas 1969) played a significant role in shaping the diversification of Amazonian peoples in pre-Columbian times. Indeed, niche construction by hunter-gatherer and farmer populations (Rowley-Conwy and Layton 2011; Hünemeier et al. 2012b) may have been important in shaping local adaptations that drove the expansion and dispersal of different indigenous groups throughout Amazonia. Other environmental and cultural aspects can also be expected to play important roles in this dynamic, such as the upper Rio Negro cultural alliance in north-western Amazonia, between Brazil and Colombia (Epps and Stenzel 2013). In the upper Rio Negro (Vaupés) region, alliances involving at least 600 years of marriage practices between indigenous groups, speaking many different languages from two independent families, have created a multi-ethnic system across an area of 250,000 km², occupied by humans since 3200 BP (Neves 1998). In contrast to the remaining areas of Amazonia, this region is expected to have developed a large and complex population made up of many patrilineal clans and tribes linked by gene-flow, due to the exchange of wives between speakers of languages of the Arawak and Tukano families.

Much of the genetic difference observed between indigenous populations in the Central Andes and in Amazonia can be accounted for by their contrasting histories of gene-flow, demic expansion and dispersal. That said, although these contrasting patterns can be recognized between the two regions, within each there is also significant heterogeneity of (biological) populations and cultural relationships, changing through time and space. Besides, there are three sets of indications that this ‘divide’ is of course not entirely abrupt or absolute: reports of historical gene-flow between indigenous groups from the Andes and Amazonia (Sandoval, Lacerda et al. 2013; Cabana et al. 2014; Barbieri et al. 2014); the existence of outlier groups in each region (Sandoval, Lacerda et al. 2013); and the absence of clear geographical and linguistic associations with genetic diversity (Callegari-Jacques
et al. 2011; Reich et al. 2012; Roewer et al. 2013). More recently, some large studies including complete genomes of modern (G necchi-Ruscone et al. 2019) and ancient (Moreno-Mayar, Vinner et al. 2018) Native Americans indicate a complex demographic scenario for the occupation of South America, with multiple dispersal events between South and Central America giving rise to indigenous populations of Andes and Amazonia (and other non-Andeans). Future studies in population genetics should significantly enrich our understanding of the origin and diversification of the indigenous populations of South America, who still bear direct cultural and genealogical connections to their pre-Columbian ancestors.