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Rosseirys De La Rosa April 12, 2022

Understanding the Evolutionary History of Ancient Indigenous Individuals in Uruguay

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Abstract
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Recent technological advances have allowed the frequent use of the human population genetics field to reconstruct human histories. Using modern and ancient DNA, genetics complements historical and archaeological accounts of population histories. In this study, human population genetics methods will be applied to further research the evolutionary history of ancient Indigenous individuals in the Uruguay region and other ancient genomes from the Americas. The objective of this study was to conduct archaeogenomic work by presenting high-coverage whole genomes from an archaeological site in Rocha, Uruguay, dating from ~1,450 to ~668 years before present. This data represents the first ancient genomic DNA from the region and could hopefully provide a starting point to examine the evolutionary history of the ancient Indigenous people of Uruguay and spark conversation about the use of genetics and identity. Sequenced DNA from the ancient individuals of interest and genomes previously published were used to answer the objective. Various computational analyses were performed, such as a principal component analysis (PCA), an admixture plot, and a maximum likelihood tree. The results from the computational studies had two interesting findings. First, in terms of relatedness between the ancient individuals of interest and other ancient individuals from the Americas, there seems to be a relationship between the ancient individuals from Brazil and Panama, as they were closely related to the ancient individuals from the Uruguay region. The results also showed that there might be an ancestral lineage in South America that has potentially never been seen before due to the lack of data in South America. These results question the concept of race and identity, making the definition more nuanced with the addition of genetics. Overall, these results broaden our knowledge of the Indigenous populations in Uruguay, allowing further conversation in the future.

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Table of Contents

Figures

"Esos salvajes hombres no son…
No tienen alma;
no son hijos de Adán, no son, Gonzalo;
esta estirpe feroz no es raza humana" (Zorrilla de San Martín et al., 1965)

"These savages are less than human…
They have no souls; They are not sons of Adam, no, Gonzalo,
No human breed is this barbarian tribe" (ibid).

Introduction

The South American country of Uruguay is known as a *"pais sin indios,"* a country with no Indians. Like many Indigenous groups in the Americas little is known about the Indigenous population that resided in Uruguay before European contact. Like other Indigenous groups, there was a decline in their population due to disease and warfare. Uruguay, however, is one of the few countries that has a narrative that for the most part does not include the presence of Indigenous groups past the mid 1800s (Sztainbok, 2010). The largest Indigenous group in the country were the Charrúa, that after several years of infighting against the Spanish were killed off in a series of campaigns known as "Salsipuedes" which translates to "get out if you can," (Sans et al., 2012). Due to the erasure of most of the Indigenous communities throughout the history of Spanish colonization in South America, the past lives of Indigenous people became a popular topic of study in Uruguay. There has been some argument between scholars on whether there was only one group of Indigenous people by the time the Spanish arrived in Uruguay. There are historical accounts from the Spanish of numerous different Indigenous groups who lived around Rio de la Plata at the time of their arrival including: the Charrúas, Yaros, Bohanés, Chanás, Archanes, Guenoas, and Minuanes (Figueira, 1892). However, as time went on, the idea of multiple Indigenous groups in Uruguay slowly faded.

Whether or not modern-day Uruguayans have Indigenous ancestry is a question that has resurfaced recently. Local activist groups in South America have claimed to have Charrúa ancestry. However, to accurately model the population history of the Indigenous communities in Uruguay requires contributions from interdisciplinary fields: anthropology, history, and archaeology. Yet, due to the lack of historical accuracy of what happened when the Spanish arrived, it is hard to definitively say whether their ancestry, if any, belongs to the Charrúa or other Indigenous groups that could have possibly been present around the same time. However, with the emergence of genomics, a different narrative can be added to the story. Due to technological advancements, the study of genomics has become popular within the last decade that has allowed the study of both ancient and modern genomes. In contrast to the history narrated by the Spanish invaders and their modern interpretations, Ancient DNA allows us to reconstruct the history of the Indigenous people from Uruguay without the biases associated with European colonization.

Ancient genomes from Uruguay have yet to be published to finally settle the debate of whether modern day Uruguayan citizens have Indigenous ancestry or not. Therefore, this thesis will address not only the history of different Indigenous communities post European contact, but it will shed light on the origins of the Indigenous people of Uruguay through the study of ancestral population and thus present a starting point to further study the evolutionary history of Indigenous Uruguayans. Using high-coverage whole genomes from an archaeological site in Rocha Uruguay, this research will create a population-specific history for the ancient Indigenous individuals using computational methods. These methods include principal component analysis (PCA), as a method to better understand the relationship between the ancient Indigenous

individuals from the Uruguay region and other ancient individuals from the Americas. Ancestry clusters, maximum likelihood trees and F3 statistics were also used to explore said relationship.

Additionally, the first chapter of this thesis will further explore the work the historical accounts regarding the Indigenous people from the Uruguay region. Focusing on the missionary work from when the Spanish first arrived, the eradication of the Indigenous population following post European contact, and archaeological work that has been done to study the past lives of the Indigenous communities. Caution has been employed regarding the possible connection between different ethnic Indigenous groups and the present population as historical evidence and archaeological evidence have not always agreed. Hence this research will set a starting point to study the evolutionary history of the Indigenous populations of Uruguay.

Literature Review

a. European Contact and Missionary Work

The start of the end for the Indigenous communities in the Uruguay region began with the arrival of Spanish missionaries in Santo Domingo Soriano, Uruguay, during the late 1500s. Spanish missionaries began the process of Catholicizing Indigenous communities and "civilizing" them, known as *reduccion* or reduction in English. *Reduccion* refers to the settlements created by Spanish rulers to reinforce the idea that the Indigenous people needed to live in urban settlements that resembled towns in Spain. During the forced conversion, numerous missionary groups were present teaching the practice of Catholicism, including the Jesuit, Carmelo, Francisco, and Dominican Order. All who played their part in incorporating and spreading the policy of reduction throughout most of South America.

There are historical accounts of numerous different Indigenous groups who lived around Rio de la Plata and the Uruguay River at the time of arrival of the Spanish explorers. The Charrúas,

Yaros, Bohanés, Chanás, Archanes, Guenoas, and Minuanes (Figueira, 1892). For the most part, according to the Spanish, their relationship was friendly. The Indigenous people were hospitable and provided food for the newly arrived Europeans. Later, insignificant events began the confrontations between both sides, and with the passing of centuries warlike confrontations between the natives and Europeans were heightened (Szilágyi Chebi, 2015). In a letter sent from Benito Lopez de Rios, who would later become the first elected mayor of the newly established town of Santo Domingo Soriano, to King Ferdinand VII of Spain, Lopez explains the early origins of the town, their relationship with the different groups of Indigenous people, and ends by asking the crown to acknowledge Santo Domingo Soriano as an official town (De-María, 1892).

The letter explains the many efforts of different missionaries in the late 1500s to civilize various Indigenous communities; Charrúa, Yaros, Bohanés, Chanás, and Minuanes. The missionary groups mentioned include the Jesuit, Carmelo, and Dominican Order. All who were present and took part in the reduction policy of the Indigenous people. The Dominican Order was supposedly successful in the reduction and conversion of the Charrúa to Catholicism. However, the letter claims that due to not wanting to leave their barbaric ways, they abandoned the settlement and moved across Rio Negro. The Spanish were however able to convert the Chaná to Catholicism and the Chaná admixed into the Spanish community (ibid). This conversion to Catholicism was supported by Jose H. Figueira, an Uruguayan anthropologist who spent some time studying the different Indigenous communities of Uruguay in the late 1800s (Figueira, 1892).

The relationship between the Chaná, Charrúa, and Spanish was a complicated one. The letter from Lopez to King Ferdinand explains that the Chaná's leader was the one who slightly

forced his people to abide by Spanish rule (De-María, 1892). Félix de Azara, a Spanish military officer who traveled frequently throughout the 17th century claimed that it was due to the protection that the Spanish could offer that most Indigenous groups agreed to the reduction. The Chaná were a small group compared to the Charrúa and they did not have the necessary resources to protect themselves from the Charrúa. Therefore, agreeing to the reduction was a strategic move to ensure their survival (Esponera Cerdán, 1992). The Indigenous communities were not the only ones who needed help from the Spanish—the Spanish also needed help from Indigenous communities. In 1624 the governor of Rio de la Plata, Francisco de Céspedes, promised the Charrúa and the Chaná good treatment if they helped them against the Dutch who were trying to take land away from the Spanish. The two Indigenous communities helped fortify a Spanish base, and in response, they were given silver for their work. Céspedes then used that built relationship to ask the Charrúa and the Chaná to agree to the process of reduction. With the help of Bishop Frey, Pedro de Carranza of the Carmelo Order alongside different church orders, helped conduct one of the largest processes of reduction seen in Santo Domingo Soriano (Marotta Castro, 2001).

The early missionary work referred to by Lopez was occurring throughout present-day Paraguay, Argentina, Southern Brazil, and Uruguay. The Jesuits from the Society of Jesus Order referred to the area as the Province of Paraquaria (Jackson, 2019) The Uruguay River and the Rio de la Plata were reference points where missionaries built settlements to encourage Indigenous communities to stay sedentary. The Guarani, who lived on the west side of the Province of Paraquaria, were an Indigenous community that frequently fought with the Spanish and Portuguese. On top of having the Jesuit Order attempting to implement their reduction policies, the Portuguese were trying to enslave the Guarani, and the Spanish attempted to

establish encomienda systems. Encomienda systems established by the Spanish gave them control over Indigenous populations where they could demand forced labor. However, if Indigenous people agreed to live in reduction towns, they were exempt from encomienda laws. The Paraquaria region is a prime example of these exemptions. Instead of the encomienda system, they established a form of tribute where Indigenous communities paid tribute directly to the Spanish King and enjoyed a variety of self-rule and land ownership (ibid).

The Portuguese constantly attacked Jesuit and Spanish settlements to gain slaves, making the Spanish the better of the two colonizers. The Spanish government offered the Guarani protection if they agreed to be Catholicized leading to the Guarani aiding the Spanish in many of their battles. At first, the Spanish were hesitant to provide the Guarani with weapons. However, after the victory at the 3 Day Battle of Mbororé in 1641, the Spanish utilized them constantly in battles. They were known as the Jesuit militia. From rebellious colonists to hostile Indigenous groups, the Jesuit military militia played a large role in keeping the peace in the Paraquaria region. Scholars argue that without the help of Indigenous communities, there would have been a low chance of South America to have the outcome it did (ibid). Indigenous bodies were expendable, they fought battles and the Spanish were the ones gaining. Although they were allowed to bear arms, the Spanish did not necessarily trust them at first. They did not want the Indigenous groups to use the weapons to start a rebellion, hence, they took precautionary measures such as routine weapons check. Another famous reduction camp was Concepción de Cayastá under the order of the Franciscans in present-day Santa Fe, Argentina. Indigenous people in this settlement went through an intense process of acculturation and were eventually integrated into the colonial Spanish community. In comparison to the Indigenous people in the Jesuit reduccion camps, those who lived in Concepción de Cayastá had very little freedom

regarding their everyday lives. The objective, according to the governor of present-day Buenos Aires, was the complete destruction of their culture (Bracco, 2016):

"El objetivo era la total destrucción de '...los indios charrúas, manchados, martianes, bojanes, y yaros [...] llegará el todo de su número, a tres mil, y de armas, a seiscientos'"

The governor speaks specifically about the annihilation of certain Indigenous groups in an attempt to reduce their numbers. He described them as "Indians", "Stained Skins", and "Martians." The governor aimed to reduce the protection that Indigenous people were getting when they escaped from one province to another. Before then, the purpose was to attempt to assimilate them to Spanish customs. However, after decades of work, it became difficult to convert all the Indigenous people in the region to Catholicism. Requiring, other methods to solve the Indigenous problem.

Although many Indigenous groups assimilated to European culture, there were still instances where they demonstrated agency. In 1632, a Jesuit priest attended a seminary during the conversion of some members of the Guarani group and saw evidence of "bone cult, shamanism, and the inclusion of traditional symbols in the churches built on the missions" (Jackson, 2021). Although the Spanish attempted to impose their religious beliefs on Indigenous communities, the Guarani were still able to hold onto their own traditions by either practicing their beliefs in private or superimposing their beliefs on the catholic religion. Allowing them to practice their own religious beliefs without straying too far from what the Spanish had been forcing them to practice. In the eradication of Indigenous communities in South America, religion played a significant role in establishing the prominence of the new phenomenon of white supremacy. Without there being a foundation to argue that the Indigenous groups were the "other" race because of their "uncivilized" ways, Europeans had no grounds to justify their

actions. By using that knowledge and form of thinking, Indigenous groups were able to work within the system put in place and protect some of their cultures and traditions from complete erasure.

In 1767, the Jesuits were expelled from South America by order of the Spanish crown. Portugal began this expulsion in 1759, France followed in 1764 and Spain were the last ones to exile the Jesuit Order forcing them to leave Spanish territory. As the members of the Jesuit order were moved throughout South America to be shipped back to Europe, they spread disease that killed hundreds of individuals (Jackson, 2021). Indigenous populations suffered greatly from the epidemic, declining their populations to the point of near extinction, both culturally and biologically. Although the missionaries left, the Indigenous groups that they converted remained living in communities that mirrored Spanish cities. By the 1700s the Spanish had been enforcing catholic ideas for about 200 years. Signifying that the Indigenous communities who did agree to go through the process of reduction, whether for protection, economic reasons, or by force, had extensively assimilated to Spanish traditions. Meaning that the lack of presence of religious orders did not affect their decision to stop practicing Catholicism. However, regardless of their religious status, Indigenous communities were still seen as inferior and a nuisance to European forces, complicating the relationship between the Spanish and multiple Indigenous groups.

b. Extinction of Indigenous Populations

As mentioned, the cordial relationships between the Indigenous communities and the Europeans did not last. There was constant fighting between the Spanish, the Portuguese, and the Indigenous people, as well as within the Indigenous communities. In the letter to King Ferdinand from Lopez cited earlier, he explains that the Chaná fought against other Indigenous groups which resulted in the extinction of the Yaros and Bohanés with little help from the Spanish

government (De-María, 1892). In the early 1800s, the first president of the Republic of Uruguay, Fructuoso Rivera, started facing pressures regarding the "Indian problem" from the newly developed government and tensions began to rise. Rivera had his own biases against the Indigenous people. He believed they were "wicked who know no restraint to contain them" and that they could not be left "to their natural inclinations" (Hugarte, 1969). In a campaign called "Salsipuedes", which translates to "get out if you can", a series of events occurred that led to the extermination of the Charrúa. These events built up to the Massacre of Salsipuedes on April 11, 1831.

There are multiple eye-witness accounts of what happened on that day. The Caiques of the Charrúa were offered several barrels of brandy and presents to intoxicate them when they were invited to meet with Rivera's troops in Salsipuedes. General Rivera had invited them to talk about defending some territory and requiring their help. Later, the Charrúas were surrounded by the troops, seizing their weapons and horses before attacking them. It is said that Rivera took the first shot leading to the massacre of roughly three hundred people, mostly women, and children. The ones who were not killed were taken as slaves, slowly admixing into the Spanish community. The next attacks were carried out by Rivera's nephew Colonel Bernabé Rivera. There were four individuals of the Charrúa who survived the first massacre and were sent to Paris to be studied. They were considered exotic and put on exhibition for the French people to gawk at. They all died in captivity with the exception of one woman who was able to escape with her daughter and disappear from historical records (Barrios Pintos, 1991). After Salsipuedes, the Charrúa were gradually dispossessed of their sovereignty while the new State was affirming its jurisdiction over the whole territory.

The massacre of Salsipuedes was not the only instance where Indigenous populations where persecuted by the Spanish. The Spanish had a great relationship with the Guaraní because of their willingness to convert to Catholicism. The Jesuit militia comprised of the Guaraní were also known for attacking Indigenous communities. An example of the Spanish using the Guaraní to fight other Indigenous groups is the Battle de Yí in 1702. The Guaraní, an armed force with military trained men attacked the Charrúa who were supposedly stealing horses from the Spanish and trading them with the Portuguese. The Charrúa were ambushed as the Guaraní attempted and succeeded in stealing their horses. The battle was not a fair fight, leading to the death of about 300 individuals and the imprisonment of 500 individuals. The Charrúa that were caught were mainly women and children and they were either sold as slaves, put in jail, or sent to Jesuit reduction camps where they were forced to convert to Catholicism. The massacre was justified by the Jesuit Order as they claimed their mission was to save the Charrúa just as they had done with the Guaraní (Yujnovsky et al., 2019).

One of the reasons the Jesuit Order was expelled from Spanish territory was so that the Spanish could control the Colonia del Sacramento, a region controlled by the Portuguese by the Rio de la Plata. The Portuguese had claimed most of modern-day Brazil and they had labor intensive agricultural work. The Jesuits missionary camps provided Indigenous communities safety if they agreed to convert to Catholicism. The Portuguese needed cheap labor to work the fields in Brazil, so one of the reasons the Spanish expelled the Jesuits was in exchange for land (Assunção et al., 1996). However, because the Jesuits no longer provided Indigenous communities with protection, whether they converted or not, the Portuguese were now free to attack them. The Indigenous people did not agree with this trade and attempted to fight back. The

governor of Montevideo at the time, Jose Joaquin de Viana, ordered their army to catch every Charrúa who seemed to oppose the treaty signed by the Spanish and Portuguese (Klein, 2007):

> *"Sujetar a los Charrúas a la cruz y a la campana o pasarlos a cuchillos a todos los varones mayores de doce años"*

The governor sought the genocide of every male Charrúa over the age of 12 and every female to be converted to Catholicism since that meant they would make model wives.

Aside from fighting against Europeans and other Indigenous groups, Indigenous communities had to focus on the diseases that Europeans brought with them. Because there was constant traveling across the country, whether it be for war or mission trips, Europeans spread many diseases. Smallpox and measles were a new phenomenon Indigenous communities had never seen before since they were diseases that had come from the "Old World" (Jackson, 2021). Some missionaries used the diseases to convert Indigenous groups to Catholicism. They claimed that the ones who got sick were the ones who refused to convert. By striking the fear of death into these Indigenous groups, the Jesuits were able to convert large numbers of Indigenous individuals to Catholicism. However, missionary camps were not free from diseases either. Because of the high population density of Indigenous individuals living in the camps, diseases spread quickly from household to household leading to many deaths. Although some developed immunity, most of those affected passed away (Ganson, 2003). Nonetheless if Indigenous groups lived in missionary camps or not, hundreds of thousands of people, European and Indigenous, were dying due to a series of severe epidemics that plagued South America.

c. Archaeological Evidence

Due to the erasure of many of the Indigenous communities throughout the history of Spanish colonization of Uruguay, the past lives of the Indigenous people became a popular topic of study

in Uruguay. A lot of excavation sites have been studied to explore the past lives of said Indigenous groups. Archaeological work began as early as Jose H. Figueira in 1892. It is important to note that due to the history of the Indigenous groups and the Spanish many of the Indigenous groups that were not killed off joined the Charrúa because they were the largest Indigenous community in present-day Uruguay. Therefore, most archaeological research refers to much of their evidence as evidence specifically for the Charrúa. Jose. H Figueira did an extensive study of the different Indigenous groups. It is important to note, however, that Figueira believed that it was necessary to destroy the Indigenous people because they were savages and had the mental capacity of children. The book he published aimed to introduce the 'primitive' cultures from the young country of Uruguay to an educated European audience, during an exposition in commemoration of the Spanish conquest of America.

Early excavations primarily focused on the "gathering" part of hunter-gatherers. A study in 1992 concluded that the Charrúa were long-term territorial groups who developed efficient economic strategies that allowed them to invest significant time and labor in earthen monuments that gave no immediate return in subsistence. Refuting the previous hypothesis that specifically the Charrúa were nomadic. In the early 2000s, evidence suggested the Charrúa had a society with a mixed economy that combined fishing, hunting, and gathering with small-scale horticulture such as maize, beans, squash, and possibly domesticated tuber (Iriarte et al., 2001). Archaeologists believed there would be an abundance of large animals and palm nuts. Further archeological investigations found ancient human remains buried alongside domestic dogs, pots, stone tools, corn seeds, pumpkins, and beans. Providing evidence for the first time of agricultural practices by the Indigenous people of the region, who were thought not to have discovered agriculture until the arrival of Europeans (Verdesio, 2008). Research done in Isla Larga revealed

starch grains from beans and rhizomes radiocarbon dated at 4190 BP, making it the earliest case of a mixed economy that included the cultivation of maize and pumpkin in southeastern South America (Iriarte et al., 2004).

Figueira explained that the Charrúa were known to have a fighting spirit after killing the Spanish explorer, Juan de Solís, and most of his party in 1512. According to Figueira, they had the darkest skin of all the Indigenous groups. They rarely got sick which allowed them to grow old. They were quick and agile which was helpful since they hunted deer and ostrich. He also noted that the Spanish missionaries rarely had the luck to get them through the process of reduction (Figueira, 1892). The Yaros, according to Figueira were hostile towards the Charrúa but, sometimes they would create an alliance to fight against the Spanish. They got their food from hunting but mostly fishing since they lived off Rio Negro. According to the Spanish, the Charrúa had killed off the Yaros but, Figueira believed that they were admixed into the Charrúa community and those who did not were eventually killed off by the Spanish (ibid). The Bohanés lived north of Rio Negro, and they were believed to speak a different language from the rest of the Indigenous groups. They were seen at first to be fighting against the Charrúa only then to have integrated into their community in the 18th century.

After the Governor, B. Garcia Ros started a campaign to exterminate the Bohanés, their names were erased from historical records (ibid). The Chanás depended on fishing and were even seen to have canoes. As mentioned earlier they assimilated to the Spanish and the number of "pure" Chanás was reduced to almost zero (ibid). The Archanes name means, "town that sees the day appear." They were often seen fighting against the Charrúa but, were completely killed off after the 17th century (Ibid). The Guenoas lived in the woods near Rio Uruguay. They hunted and fished as well for food. A lot of them went through the process of reduction and by order of

Governor B. Garcia Ros, was told to fight other Indigenous groups. They admixed into Spanish and Portuguese societies sometimes even joining their armies (ibid). The Minuanes lived in west Uruguay. They traveled southeast to join forces with the Charrúa and fight the Spanish. Because of this, they were often confused with the Charrúa or sometimes Guenoas (ibid).

Numerous amounts of archaeological work has been done after Figueira. In 1986, a series of excavations of Cerritos were found in eastern Uruguay. Cerritos are structures made from Earth and clay that indicate human interaction with the environment. Human and other remains found in several cerritos suggest that the Charrúa held some type of funeral function (Mazz, 2001). There were also different items buried with different individuals suggesting social complexity (Mazz et al., 1992). The cerritos were mainly interpreted as burial sites at first but, after more research, it was agreed that the cerritos were a multifunctional space used systematically to live, bury, and cultivate food in southern Brazil and Uruguay (Milheira & Gianotti Garcia, 2018).

Uruguay offered a lithic-rich environment for past Indigenous cultures in South Brazil and Uruguay, otherwise known as the Southern Cone. Figueira had made observations about lithic raw materials and published photographs about several lithic artifacts found in various surface sites around the country. Regarding lithic procurement, Figueira believed in the possibility of long-distance transport, but without specifying the types of rock obtained in such a manner (Figueira, 1892). Earlier archaeologists that focused on lithic technology also noticed that there could have been a trading system because they were digging up rocks that were not native to the region. Using geography and general observations, archaeologists divided Uruguay into five distinct regions. The northern region had silicified sandstones, including basalt for grinding and chalcedony for knapping. The northeastern area had silicified wood and limestone for knapping. And effusive rocks and granite for grinding. The central region had chalcedony and silicified

limestone for knapping and basalt for grinding. The south and southeastern area had quartz and chalcedony for knapping. And metamorphic and granite rocks for grinding. Finally, the western region had silicified limestone for knapping and basalt and granite for grinding purposes (Batalla, 2016). A comparison of the distinct raw materials taken from various parts of the region confirmed certain areas as the source area for different artifacts. Long-distance transport of between 400 and 500 km could have implied extended social networks between early hunter-gatherers of the Southern Cone (ibid).

There is a lot of evidence from both lithic technology and archaeological excavation that imply that, contrary to popular belief in the past, the Indigenous people in the Uruguay region had a complex trading system as well as a complex societal system. There were many Uruguayans like Jose H. Figueira that believed that the Indigenous people of the land got what they deserved. A Uruguayan poet referred to as "*El Poeta de la Patria*" or the "National Poet of Uruguay", Juan Zorrilla de San Martín, wrote a poem "Tabaré" where he explained how the Charrúa went extinct because they were incapable of understanding and adapting to the Western capitalist way of life (Martín, 1930). However, today, there are multiple groups in Uruguay that call themselves the descendants of the Charrúa. There is a nascent campaign emerging who want the government of Uruguay to recognize them as a people and as victims of cultural genocide. There is some disagreement, however, on whether the people living in Uruguay are only descendants or if they have a direct lineage to the ancient Charrúa (Nolen, 2018).

III. Methods

a. Objectives

To conduct archaeogenomic work by presenting high-coverage whole genomes from an archaeological site in Rocha, Uruguay, dating from ~1,450 to ~668 years before present,

representing the first ancient genomic DNA from the region and providing a starting point to examine the evolutionary history of the ancient Indigenous people of Uruguay.

b. Archaeology and Samples

The Department of Biological Anthropology and Faculty of Humanities and the Sciences of Education, in the University of the Republic of Uruguay, located in Montevideo, Uruguay, performed the archaeological work. From the 1980s, the department focused on the *cerritos* structures mentioned in the literature review. "*Cerritos* de Indios" are mound structures that show complex socio-cultural processes involving the local population from more than 5000 years ago. Evidence of *cerritos* shows that they were occupied until the 17th century. At the same end point, Europeans arrived in the area. The mounds are evidence that hunter-gatherer groups lived in the area, practicing some form of horticulture. The presence of skeletal remains is prevalent in *cerritos.* There is a multitude of archaeological evidence of human burials in these structures. The skeletal remains recovered from the *cerritos* have focused on various genetic studies, such as ancient mitochondrial DNA. More specifically, one group looked at the genetic diversity of Native American lineage present in current Indigenous and nonindigenous admixed populations to estimate the effective population size of contemporary and pre-European contact Indigenous populations (Tavares et al., 2019). The two samples presented in this research are from the site CHD01 in Rocha, Uruguay, a group of two mounds (A and B).

Human remains from the site CHD01 showed evidence of belonging to the haplogroup C1d3, a variant found only in Uruguay and the current Uruguayan population. Radiocarbon dating, date mound A and the samples recovered at about 2000BP, the time of European contact. The mound is approximately 1.20 m high with a diameter of 35 m. It is presumed to be a small part within a broader site of about 20,000 square meters. Archaeological materials found in mound A show

activity in surrounding areas. However, there is ongoing debate between biological and cultural anthropologist about the exact mechanisms, formation, and purposes of *cerritos,* allowing no definitive interpretation regarding site CHD01. In the excavation site IA, a 25 square meter dig was carried out in the center of mound A. Several bone assemblages representing the primary and secondary burials of at least 21 individuals were recovered from the site.

c. Ancient DNA Extraction

The two ancient tooths excavated from site CHD01 were extracted and sequenced in the Lindo Ancient DNA Laboratory located in Emory University using the Dabney protocol (Dabney et al., 2013). Before beginning the drilling protocol, the lab space is thoroughly decontaminated using bleach and DNA-off. All materials are exposed to UV radiation for 15-20 minutes before using, including drill, drill bits, weigh boats, isopropanol, molecular grade, foil, and tubes. The reasoning behind using bleach to avoid contamination is because bleach creates nicks across the backbone of DNA inhibiting modern contaminants from being amplified. UV radiation is also effective in preventing modern DNA contamination because UV light creates dimers between two adjacent thymine nucleotides creating a kink in the DNA chain. Similar to bleach, UV-exposed DNA contaminants would not be amplified in downstream steps since the DNA polymerase cannot read the DNA.

After decontamination, the teeth are labeled, quickly wiped with bleach, washed, and dried. Each tooth is then exposed to UV radiation on each side for ten minutes to lower the risk of contamination. The teeth are drilled in a drill hood to contain bone powder that might disperse during drilling. Each tooth is drilled, while avoiding the enamel, until 0.1g of bone powder is collected. Each tooth is drilled separately, and the drill hood is cleaned with bleach after each

sample. When done drilling, the surface is disinfected again with bleach and DNA-off (TakaraBio).

The samples are then prepped for the first part of DNA extraction. An Extraction Buffer, Binding Buffer, and TTE Buffer are made and exposed to UV radiation for 30 minutes (the 50mL tubes they are made in are also UV'd). 975uL of Extraction Buffer and 25uL of Proteinase K (Prot K) are added to each sample. They are incubated in a rotator for 24h at 37˚C. The role of Prot K is to digest proteins in the cell that could damage the already degraded DNA during the rest of the extraction. The Extraction Buffer breaks open the cell to allow the Prot K to digest all proteins. After a 24h incubation period, the samples go through a process of binding, washing, and isolation through multiple steps in the protocol. The DNA extract is then stored and placed in the freezer @ -20ºC.

d. DNA Sequencing

Libraries were prepared using NEB Ultra II DNA Library Prep for Illumina, with modifications for ancient DNA, including quartering the reagents, the use of 1:20 adaptor dilution, and 1.5ul of premixed NEB indexes. DNA sequencing is the process of determining the exact order of DNA base pairs (A, C, G, T). The data is then analyzed and interpreted using different computational programs. The first round of screening was done in the Lindo Lab, looking for endogenous DNA on the Illumina iSeq 100 and not treated with the USER enzyme. The samples chosen for deeper coverage were sequenced on the NovaSeq 6000 at Dante Labs in L'Aquila, Italy. Those samples were treated with the USER enzyme to compensate for any DNA damage. USER enzymes are uracil-DNA-based enzymes that repair DNA damage.

The raw ancient samples were trimmed for Illumina adapters using AdapterRemoval2 (Schubert et al., 2016). A common problem with short-read sequencing is adapter contamination,

often disturbing the downstream analysis of the data. This program efficiently removes adapter contamination. The sequences were then aligned to the hg19 human reference sequence using the BWA mem algorithm (Li & Durbin, 2009). The hg19 human reference are DNA sequences sequenced as part of the Human Genome Project, an international project to discover the complete set of human genes and make them more accessible for future biological studies. The BWA mem algorithm is an algorithm that efficiently aligns short sequencing reads with broader references, such as the human reference genome hg19, allowing for mismatches and gaps. The ancient authenticity of sequences not treated with the USER enzyme were validated with the package MapDamage2 (Jónsson et al., 2013). The package MapDamage2 identifies patterns from next-generation sequencing (NGS) and authenticates whether the sequences are ancient by identifying elevations of C to T and G to A transitions at the end of the reads, which are characteristic of ancient DNA damage. Both ancient individuals showed deamination patterns consistent with ancient DNA.

The program ARIADNA was used to call the genotypes of the ancient DNA samples. ARIADNA detects single nucleotide variants (SNVs) in ancient DNA to differentiate between mutations in the samples and contamination or DNA damage that might have occurred throughout the process (Kawash et al., 2018). The resulting VCF was further filtered to remove genotype calls with allele counts below 3. Sample CH19B showed a moderately high contamination rate, so it was then further filtered with the program RFMix (Maples et al., 2013). With the use of a reference panel, RFmix can identify haplotypes that match reference populations. We used the program to identify sites that exhibited a high probability of deriving from Europeans, which is a likely source of contamination. The VCFs for each sample were

merged with modern and ancient samples from the Americas using bcftools, a package that manipulates vcf files. These files were used to run multiple computational analyses.

Sample ID	Location	Source	Ancient/Modern
Ayayema (A460)	Patagonia, Chile	Moreno-Mayar, et al., 2018	Ancient
Spirit Cave (AHUR_206)	Nevada, USA	Moreno-Mayar, et al., 2018	Ancient
Lovelock2	Nevada, USA	Moreno-Mayar, et al., 2018	Ancient
Lovelock3	Nevada, USA	Moreno-Mayar, et al., 2018	Ancient
Sumidouro5	Lagoa Santa, Brazil	Moreno-Mayar, et al., 2018	Ancient
USR1	Alaska, USA	Moreno-Mayar, et al., 2018	Ancient
Anzick1 (Clovis)	Montana, USA	Rasmussen, et al., 2014	Ancient
Panama (PAPV173)	Coco del Mar, Panama	Capodiferro, et al., 2021	Ancient
IL2 (Rio Uncallane)	Ilave, Peru	Lindo et al., 2018	Ancient
IL3 (Rio Uncallane)	Ilave, Peru	Lindo et al., 2018	Ancient
IL7 (Rio Uncallane)	Ilave, Peru	Lindo et al., 2018	Ancient
S_Pima-1	Mexico	SGDP	Modern
S_Pima-2	Mexico	SGDP	Modern
S_Mixtec-1	Mexico	SGDP	Modern
S_Mixtec-2	Mexico	SGDP	Modern
B_Mixe-1	Mexico	SGDP	Modern
S_Mixe-2	Mexico	SGDP	Modern
S_Mixe-3	Mexico	SGDP	Modern
S_Zapotec-1	Mexico	SGDP	Modern
S_Zapotec-2	Mexico	SGDP	Modern
S_Mayan-1	Mexico	SGDP	Modern
S_Mayan-2	Mexico	SGDP	Modern
S_Piapoco-1	Colombia	SGDP	Modern
S_Piapoco-2	Colombia	SGDP	Modern
S_Quechua-1	Peru	SGDP	Modern
S_Quechua-2	Peru	SGDP	Modern
S_Quechua-3	Peru	SGDP	Modern
S_Karitiana_1	Brazil	SGDP	Modern
S_Karitiana_2	Brazil	SGDP	Modern
B_Karitiana_3	Brazil	SGDP	Modern
S_Surui_1	Brazil	SGDP	Modern
S_Surui_2	Brazil	SGDP	Modern

Figure 1: List of all populations used in analysis

IV. Results & Discussion

To assess the relationship of the ancient Uruguayan individuals with global and regional populations, the datasets created were merged with modern genomes from the Simons Genomes Diversity Project (Mallick et al., 2016) and ancient whole genomes from the Americas. All genomes used are listed in Figure 1 above.

a. Principal Component Analysis (PCA)

A principal component analysis was performed to understand the relationship of the ancient individuals from Uruguay with other ancient individuals from the Americas. A principal component analysis is a type of statistical cluster analysis used to higlight variables attributed to the greatest variation in a dataset.

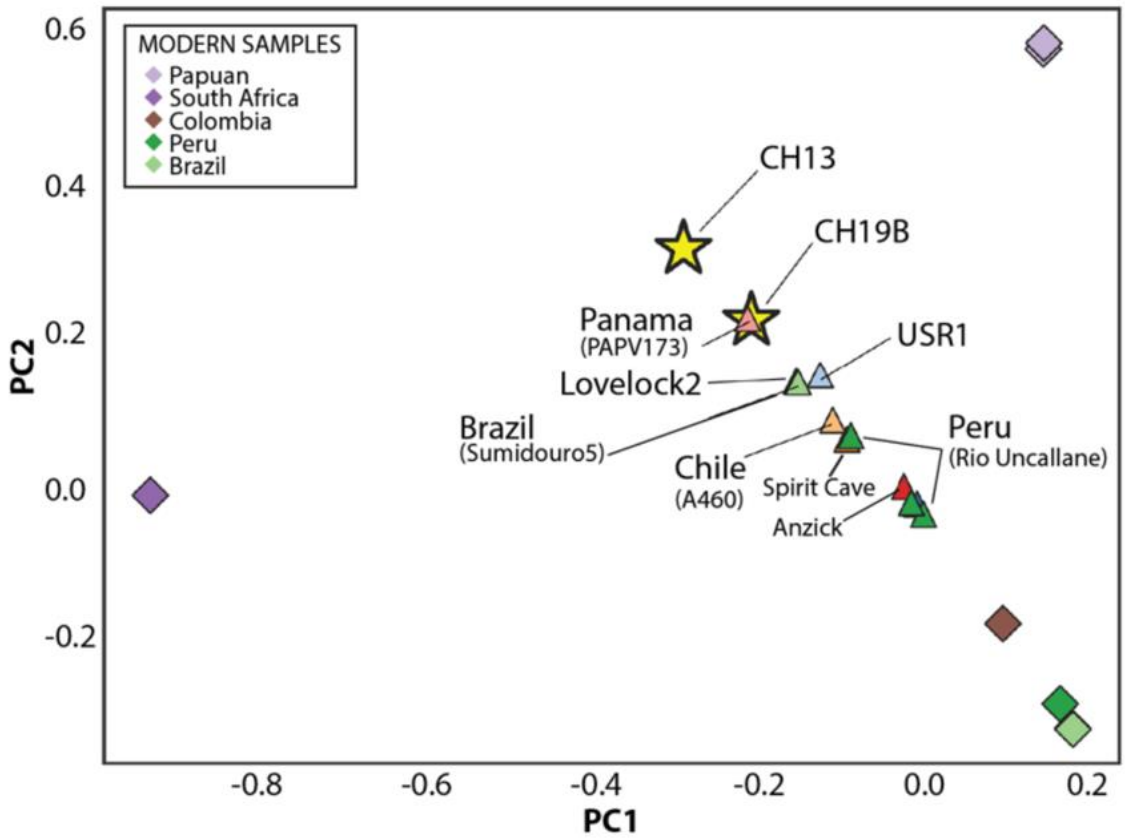

Figure 2: PCA Projection of Indigenous individuals from the Uruguay region. Diamonds indicate modern samples and triangles indicate ancient samples

The PCA in Figure 2 reveals the interrelatedness between ancient individuals in South America and the ancient Indigenous individuals of interest, clustering by genetic similarity. As seen in Figure 2, the Indigenous individual from the Uruguay region dated at ~1400BP shows a strong affinity with the ancient individual from Panama PAP173, dated at ~600BP. While CH13, an Indigenous individual from the Uruguay region also dated at ~600BP, demonstrates a more distant relationship with the ancient individuals. The relationship between CH19B and PAP173 shows that there could potentially be shared ancestry between two individuals who live on opposing sides of the continent.

b. Admixture

To further study the shared ancestry between Indigenous individuals from the Uruguay region and ancient individuals used in the study, ADMIXTURE (Alexander et al., 2009) was used to generate ancestry clusters. Admixture is used to infer ancestral relationships based on genetic ancestral data. The *K* value is an ideal hypothesized number of subpopulations that make up the total population. Individuals in the dataset are grouped into ancestry clusters based on allele frequency spectra. *K* values are chosen using the cross-validation method, which enables rational choice of ancestral populations. Each individual then receives an ancestry fraction for each of the ancestral subpopulations, creating the admixture graph seen in Figure 3. In Figure 3,

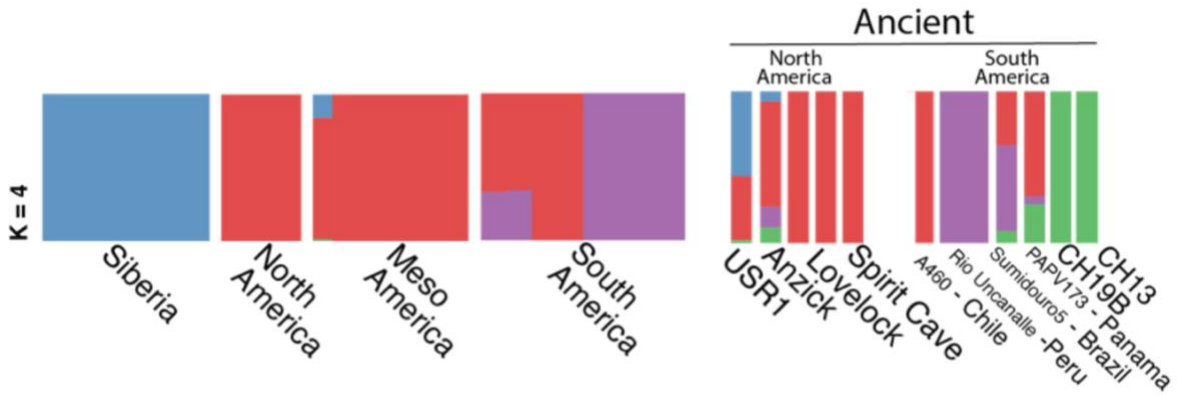

Figure 3: Ancestry clusters generated with ADMIXTURE of modern and ancient genomes

the Uruguayan green cluster is displayed in both North and South American individuals. In North America, Uruguayan ancestry is shared with Anzick (located in Montana), dated at ~11500BP, and USR1 (located in Alaska), dated at ~12500BP. In South America, Uruguayan ancestry is shared with Sumidouro5 (located in Brazil), dated at ~10000BP, and PAP173 dated at ~600BP (located in Panama).

The shared ancestry between the Indigenous individuals from the Uruguay region and various individuals throughout the Americas begins to question the validity of the "Native American" racial category. As seen in Figure 4, Anzick and the Indigenous individuals from the Uruguay region are far from each other demographically and in age. However, regardless of the distance and age difference, there is still shared ancestry between the two. The same goes with USR1 and the Indigenous individuals from the Uruguay region. The ancient individuals from South America also share ancestry with the Indigenous individuals from the Uruguay region. Although Uruguay is demographically in the same continent as PAP173 and Sumidouro5, there is still a significant distance between the individuals, the furthest one being PAP173. The time gap between the individuals adds more nuance to the

Figure 4: Map of ancient and modern whole genomes used in this study

concept of "Indigenous ancestry." Before European contact, there was no such thing as countries or political borders. According to historical records, the Indigenous populations in Uruguay were nomadic. As a group, they traveled together to different regions based on the resources in an area. With the arrival of the Europeans, however, available resources decreased, which could have potentially pushed Indigenous groups to interact more often than before European contact.

c. Maximum Likelihood Tree

Using whole-genome sequencing data from the Simons Genome Diversity Project a maximum-likelihood tree was created by TreeMix (Pickrell & Pritchard, 2012) to further explore the individual relationships between the ancient Indigenous individuals from the Uruguay region and the rest of the individuals from the Americas. A maximum likelihood tree is a phylogenetic tree where the nodes (where the branches meet) represent the most recent common ancestral population. The maximum likelihood tree in Figure 5 shows the most common ancestral population between ancient and modern individuals. Figure 5 shows a connection between the ancient samples from eastern Brazil, Panama, and the Indigenous individuals from the Uruguay region, forming their own branch. Though we cannot make a definitive statement claiming a relationship between the ancient and modern samples, the tree validates the positioning of the individuals by grouping

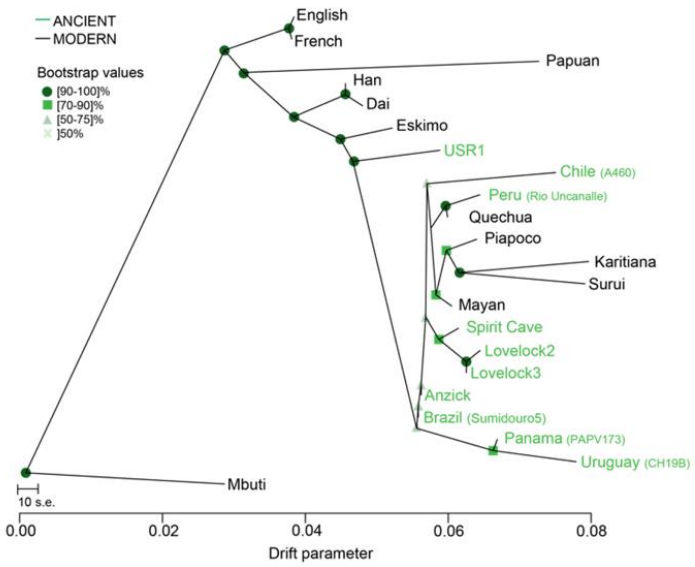

Figure 5: Maximum Likelihood Tree displaying most common recent ancestors between ancient and modern samples.

ancient and modern Peru. Additionally, the individual from Alaska (USR1) is an outgroup to the individuals from the Americas. Further validating the positioning of individuals on the tree.

Historically speaking there has commonly been an idea of uniformed Indigenous groups. When Europeans first contacted Indigenous groups, European anthropologists grouped different Indigenous populations together creating inaccurate historical accounts of said groups. Eventually these misconceptions led to the internal subdivision and categorization of the human species. Also known as the concept of race. The attempt to categorize humans into certain boxes becomes increasingly difficult when there is more than one box to check. Furthermore, as research being done in South America increases, a more nuanced story regarding human categorization unfolds.

d. Genetics & Identity

As mentioned earlier, the purpose of the PCA was to understand the relationship of the ancient Uruguayan individuals with other ancient individuals from the Americas. Individuals grouped on a PCA suggest being genetically similar to each other. Therefore, because one of the Indigenous individual from the Uruguay region aligns closely with the individual from Panama, as shown in Figure 2, it can be inferred there is a connection between the two. The results of the PCA conflict immediately with the concept of the Hispanic race. As mentioned, the distance between Panama and Uruguay is significant. On top of that, the older Indigenous individual from the Uruguay region is the sample that clustered with PAP173, regardless of being almost 600 years apart. The younger Indigenous individual from the Uruguay region is further placed from both the individuals. The distance can be for different reasons. One reason being, there could have been a large population replacement between the time period of the CH19 and CH13B. Second, the individuals could belong to different ancestral groups conflicting with the historical

common perception of one existing Indigenous group that lived in Uruguay. Categorizing all Southern Americans into a set box does not accurately represent the diversity within the country, specifically in terms of Indigenous diversity.

The categorization of race can be questioned again when looking at the ancestry clusters in Figure 3. The individuals, Anzick and USR1, are in North America. A region that even today, for the most part, does not identify as Hispanic. Yet, they seem to have some shared ancestry between the four of them. The reasoning behind the shared ancestry can be due to several reasons such as migration. However, with the age difference between the individuals and the distance, it is interesting that there is a possibility of such connection. With these connections between the individuals, the idea of "Indigenous ancestry" can also be questioned. Although the hypothesis from Figure 2, that the two Indigenous individuals from the Uruguay region may be from different ancestral groups cannot be proved by the ancestry clusters, it does reinforce the idea that humans cannot be cleanly organized into specific categories. Something else interesting about the green ancestry cluster is that the green cluster do not appear with the modern "South American" section. South America is only red and purple. With the appearance of the green cluster in ancient samples, one can infer that the Indigenous individuals from the Uruguay region demonstrate an ancestry lineage that has potentially never been seen in South America before in living populations. Because it does not show in the modern ancestry clusters this can mean a couple of different things. The first is the particular ancestry lineage associated with Uruguay is only seen in ancient individuals, explaining why only the ancient individuals have the green ancestry cluster. The second reason can be there is simply not enough genomic data on South American both ancient and modern.

The purpose of the maximum likelihood tree as explained earlier, is to further visualize the relationships between the ancient and Indigenous individuals from the Uruguay region. The ancient individual from Brazil is related to Panama and Uruguay forming their own branch on the tree. It is significant because people from Brazil are Amazonian Indigenous people who are known for their unique culture and minimal European influence. However, the ancient individual Sumidouro5 has shown through multiple analysis to have some relation to the Indigenous individuals from the Uruguay region. In the admixture analysis the Brazilian individual also shared some ancestry with Panama. A reason for this connection could be the fact that prior to strict country borderlines, Indigenous populations were nomadic. As is supported through historical records of European colonizers, Indigenous populations traveled a lot within the region especially with the changes of seasons. Indigenous populations also had to migrate when European colonizers forcefully removed them from their native land.

Spanish colonizer José Figueira noted that different Indigenous groups within the young country of Uruguay had varying phenotypical markers. However, even after admitting the different groups had distinctive customs and did not regularly admix populations, he explains regardless, they were all clumped into a category by the Spanish (Figueira, 1892).The genomic data presented in this study show how problematic the categorization of humans is. There is no clear black and white box that can be filled out especially when looking at ancestry. Said categorization only works well with European individuals since there is more genomic data on Europe than there is on any other group of people. This phenomenon is seen in popular ancestry tests such as 23andMe and AncestryDNA. The results of industry ancestry testing depend on a multitude of things, such as the size of the company's database and the genetic knowledge said industries have. Because most ancestry testing companies have a larger reference database of

European genomes, any other area in the world is less reliable and accurate. The results of these tests further complicate the concept of race since an ancestry test alone is not adequate enough to categorize humans into specific races (Jones & Roberts, 2020).

V. Conclusion

The goal of the study was to provide a starting point for the study of the evolutionary history of ancient Indigenous individuals from the Uruguay region. Using principal component analysis (PCA), admixture, and maximum likelihood tree, I am able challenge the definition of ancient Indigenous ancestry. The results of the analysis showed there is no real set definition of ancient Indigenous ancestry due to the lack of data on the subject matter. The different analysis showed an interrelatedness between ancient Panamanian, Brazilian and Uruguayan individuals about 600 years apart in age. The scarcity of genomic data on Indigenous individuals in South America further complicated the ability to have conclusive results. The results, however, question the modern concept of race and Indigenous ancestry because of such nuanced results.

To further the question of Indigenous ancestry, additional research should be done in the collection and sequencing of both ancient and modern Indigenous individuals, especially from South America. By increasing the number of genomes available for analysis, a more accurate representation can be made of the population history of the region. Furthermore, another line of inquiry could evaluate how Indigenous genomes have changed since European contact to study health related factors.

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