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# The importance of anthropological genetics research in Honduras, Central America

# La importancia de la investigación en antropología genética en Honduras, América Central

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**Abstract**

With its unique geographic location at the northern end of the Central American isthmus, Honduras straddles the boundaries of two distinct cultural regions—the Mesoamerican and the Istmo-Colombian. In this context, we briefly discuss the progress of population genetics studies conducted within Honduras.

The text underscores the importance of conducting fieldwork to improve our understanding of the genetic history, population dynamics, and emergence of diseases among the Indigenous communities of this country. Among the seven distinct Indigenous populations currently under genetic investigation, we highlight the case of the Garifuna people. We explore their origins, patterns of migration, genetic differentiation, and the prevalence of Hypertrophic Cardiomyopathy (HCM), which may be linked to founder effects.

Our research endeavors in Honduras emphasize the value of an interdisciplinary approach in the study of local human populations that have been instrumental in shaping our evolving comprehension of the genetic landscapes within this unique geographical and cultural setting. Rev Arg Antrop Biol 26 (2), 084. https://doi.org/10.24215/18536387e084

KEYWORDS: Central America; Honduras; anthropological genetics; founder effect; fieldwork

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**Resumen**
Con su ubicación geográfica única en el extremo norte del Istmo Centroamericano, Honduras se encuentra en los límites de dos regiones culturales distintas: la Mesoamericana y la Istmo-Colombiana. En este contexto, discutimos brevemente el progreso de los estudios de genética de poblaciones realizados en Honduras.

El texto subraya la importancia del trabajo de campo para mejorar nuestra comprensión de la historia genética, la dinámica de las poblaciones y la aparición de enfermedades entre las comunidades indígenas de este país. Entre las siete poblaciones indígenas que actualmente se encuentran bajo investigación genética, destacamos el caso del pueblo garífuna. Exploramos sus orígenes, los patrones de migración, la diferenciación genética y la prevalencia de la Miocardiopatía Hipertrófica (MCH), posiblemente vinculada al efecto fundador.

Nuestros esfuerzos de investigación en Honduras enfatizan el valor de la colaboración interdisciplinaria en el estudio de las poblaciones humanas locales, los cuales son fundamentales para comprender la evolución de los paisajes genéticos dentro de este entorno cultural y geográfico único en la región. Rev Arg Antrop Biol 26 (2), 084. https://doi.org/10.24215/18536387e084

PALABRAS CLAVE: América Central; Honduras; genética antropológica; efecto fundador; trabajo de campo

## BACKGROUND OF ETHNIC POPULATION STUDIES IN CENTRAL AMERICA

### The Central American Region

The Central American Isthmus, comprising Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama, constitutes a region of extraordinary ecological, geographical, and cultural significance. Its strategic position as a land bridge between North and South America, along with a wide range of ecosystems, has fostered rich biodiversity, accounting for an estimated 5–12% of the planet's biodiversity (Eiserhardt *et al*., 2017; Hall & Brignoli, 2003; Morales-Marroquín *et al*., 2022).

From a geographical perspective, the Central American Isthmus boasts extensive coastlines along the Pacific Ocean and the Caribbean Sea, as well as varied topography that includes mountain ranges, volcanoes, and wetlands. This unique geographical configuration has made the Central American Isthmus a critical area for understanding the ecological, evolutionary, and human demographic processes associated with tropical regions. As a land bridge connecting North and South America, the Isthmus has facilitated the exchange and interaction of flora, fauna, and human populations between the two continents, making it a vital region for studying the dynamics of biodiversity and human migration in the Americas (Cano *et al*., 2022; Eiserhardt *et al*., 2017; Kennett *et al*., 2022; Kistler *et al*., 2020; Prufer *et al*., 2019; Rosenswig *et al*., 2014).

In terms of its cultural dimension, the region has been home to diverse ethnic groups throughout its history, from pre-Columbian and extant Indigenous populations to present-day national populations shaped by the admixture resulting from Spanish colonization. Additionally, this region played a fundamental role as a bridge for the migrations that colonized South America during the early peopling of the Americas, as well as later migrations between North and South America (Cooke, 2021).

## Bioanthropological Research

The study of present and pre-Columbian populations in this region is crucial, as it provides insights into their origins and microevolution, as well as their adaptations to diverse environmental conditions within a relatively small territory, contrasting with the vast expanses of North and South America. The genetic relationships among extant and extinct indigenous populations, in relation to those of southern Central America, Mesoamerican cultural areas, and northern South America, remain poorly understood. This significant knowledge gap impedes our comprehension of the complex population dynamics and genetic affinities across these interconnected regions. Further research is essential to elucidate the phylogenetic connections and potential gene flow patterns among these diverse groups, which could provide valuable insights into historical migration routes, settlement patterns, and processes of cultural differentiation.

In the early 20th century, pioneering studies on human variation in Central America laid the foundational groundwork for the field of human population genetics in the region. According to Baldi and Barrantes (2019), the advancement of these studies in Central America can be divided into three distinct historical phases.

The first phase, spanning the 1920s to the 1960s, primarily relied on the use of anthropometric measurements (e.g., body proportions, cranial measurements) and classical genetic markers (e.g., blood groups, protein polymorphisms). However, these early studies often operated under the assumption of fixed racial characteristics and did not adequately consider the significant role of evolutionary processes—such as mutation, gene flow, genetic drift, and natural selection—in shaping the genetic diversity of Indigenous populations (D'Aloja, 1939; Hrdlička, 1926; Matson & Swanson, 1963; Schultz, 1926).

The second phase, spanning the 1970s to the 1990s, marked a shift towards incorporating statistical methods and extensive fieldwork to elucidate the genetic structures resulting from inter-ethnic contact or isolation. This phase shedded light on the microevolutionary effects of migration and selective pressures on various populations, such as the Garifuna in Honduras and the Indigenous populations from southern Central America. Researchers began to investigate how factors like population movements, admixture, and environmental pressures influenced the genetic makeup of these communities (Barrantes *et al*., 1982; Crawford, 1983a; Thompson *et al*., 1992).

During the third phase, extending to the present day, the advent of molecular biology techniques has revolutionized the study of genetic polymorphisms in Central American populations. Researchers have employed a wide range of molecular markers, including short tandem repeats (STRs), single nucleotide polymorphisms (SNPs), whole genome sequences (WGS), and ancient DNA (aDNA) (Capodiferro *et al*., 2021; Kennett *et al*., 2022; Mathias *et al*., 2016; Morales-Arce *et al*., 2017). These advanced methods offer greater precision and allow for a more comprehensive examination of genetic variation within and between populations at local and continental levels (Melton *et al*., 2013; Posth *et al*., 2018). Numerous genetic studies on Indigenous populations using parental markers (mtDNA, Y-DNA), SNPs, and aDNA have been conducted from the 1990s to the present. These studies have primarily focused on Chibchan-speaking populations in Panama, Costa Rica, and Nicaragua, with fewer studies conducted in Honduras, El Salvador, and Guatemala (Baldi & Crawford, 2016; Capodiferro *et al*., 2021; Melton *et al*., 2013).

More recently, the introduction of next-generation sequencing (NGS) technologies, which enable high-throughput and cost-effective sequencing of entire genomes, has been a major advancement in this field (Satam *et al*., 2023), providing significant opportunities for anthropological research in Central America.

The integration of genomic data with anthropological, archaeological, and linguistic evidence has deepened our understanding of the complex processes that have shaped the genetic landscape of Central American human populations over time. These multidisciplinary approaches have illuminated topics such as the peopling of the Americas, ancient migration routes, and the impact of European colonization and the transatlantic slave trade on the genetic diversity of the region (Capodiferro *et al*., 2021; Fortes-Lima & Verdu, 2021; Kennett *et al*., 2022).

## Fieldwork in Honduras

Qualitative research during sample recollection is essential for assessing both sociocultural and biological features of the populations under study, complementing findings from biological markers. Through immersive fieldwork, researchers can analyze populations and identify similarities and differences in phenotypic (observable traits) and genotypic (genetic) patterns shaped by diverse environments, evolutionary histories, and cultural practices. Additionally, fieldwork allows for the examination of evolutionary changes within populations over time, enabling researchers to track genetic shifts, admixture events, and the effects of demographic processes across generations. By embedding themselves within the communities they study, researchers can gain a deeper understanding of the social and demographic structures that are key to revealing the etiology (causation) of genetic transmission, especially for complex phenotypes influenced by both genetic and environmental factors (Crawford, 2006, 2024).

Ethical considerations are a cornerstone of fieldwork in biological anthropology, requiring rigorous adherence to the highest standards to protect participants' rights and anonymity while advancing scientific knowledge responsibly. Researchers must always comply with the three fundamental principles for human subject research as delineated in the Belmont Report: respect for persons, beneficence, and justice (US Department of Health and Human Services, 1979). These principles respectively ensure individual autonomy, maximize benefits while minimizing harm, and promote the fair distribution of research burdens and benefits across populations.

In accordance with contemporary ethical guidelines, such as those established by the American Anthropological Association (2012) and the World Medical Association's Declaration of Helsinki (2013), researchers must implement a comprehensive informed consent process. This process, overseen and approved by an institutional ethics committee, requires that each potential participant be fully informed about the study's purpose, methods, risks, and benefits. Participants must demonstrate understanding and provide voluntary consent before any data collection begins.

The informed consent process in biological anthropology is particularly nuanced due to the potential cultural and genetic sensitivities involved. Researchers must exercise cultural competence, ensuring that consent procedures are culturally appropriate and understandable to participants from diverse backgrounds (Guillemin *et al*., 2018). This may involve translating materials into local languages, using culturally relevant explanations, and respecting community decision-making processes where applicable.

Furthermore, given the often-sensitive nature of genetic data collected in bioanthropological studies, researchers must implement robust data protection measures. This includes secure storage of biological samples and genetic information, stringent anonymization protocols, and clear policies on data sharing and future use (Pullman & Nicholas, 2011). Researchers should also be prepared to address the potential implications of genetic findings for individuals and communities, including provisions for returning results when appropriate and managing incidental findings.

By adhering to these ethical standards and consistently reflecting on the moral implications of their work, bioanthropologists can ensure that their research not only advances scientific understanding but also respects and protects the dignity, rights, and well-being of the individuals and communities they study.

In the past, the acquisition of biological and cultural data for the study of remote and traditional populations was limited. However, notable contributions from pioneering researchers have laid the groundwork for this field. These include Ramiro Barrantes' research on Indigenous populations in Costa Rica and Panama, as well as Michael Crawford's work among the Black Caribs [Garifuna] (Barrantes, 1993; Crawford, 2024).

During the 1980s, multidisciplinary investigations in the biomedical and evolutionary domains focused on examining the genetic structure of various Indigenous groups and exploring evolutionary responses to environmental pressures in Costa Rica and Panama (Barrantes, 1993). This multifaceted research initiative encompassed comprehensive demographic analyses—including age structure, fertility rates, and mortality patterns—alongside detailed examinations of genealogical and kinship systems. Furthermore, it involved investigations into the selective pressures exerted by endemic and epidemic diseases, as well as the role of nutritional factors in population health and adaptation. Throughout these studies, extensive fieldwork provided a valuable opportunity to integrate quantitative biological data with qualitative *in situ* observations of customs and lifestyles. This integrative approach, combining molecular genetic techniques with traditional anthropological methods, enables a more nuanced understanding of the complex interplay between biological, environmental, and sociocultural factors shaping these populations.

Concurrently, Michael Crawford's fieldwork among the Garifuna included the collection of biological and demographic data from Livingston, Guatemala, and St. Vincent Island. Subsequent research extended to Honduras, Belize, Guatemala, and the Bay Islands, incorporating DNA markers such as mitochondrial DNA (mtDNA), non-recombining Y-chromosome (Y-DNA), autosomal single nucleotide polymorphisms (SNPs), and short tandem repeats (STRs). These genetic data were employed to reconstruct the genetic ancestry, admixture, and population structure of the Garifuna, yielding valuable insights into their biological and cultural heritage (Crawford, 2024).

## Honduran populations

This section provides a comprehensive overview of the general historical, cultural, and demographic characteristics of the seven indigenous populations in Honduras that form the focus of our anthropological investigations (Fig.1).

Honduras holds a unique geographic position at the northern end of the Central American Isthmus. It spans two distinct cultural regions: Mesoamerica and the Isthmo-Colombian area. The Mesoamerican region includes the western and southwestern parts of the country, where Indigenous groups connected to the larger Mesoamerican cultural sphere reside. In contrast, the eastern region is home to populations of Chibchan and Misumalpan origin (Constenla Umaña, 1991; Hoopes & Fonseca, 2003).

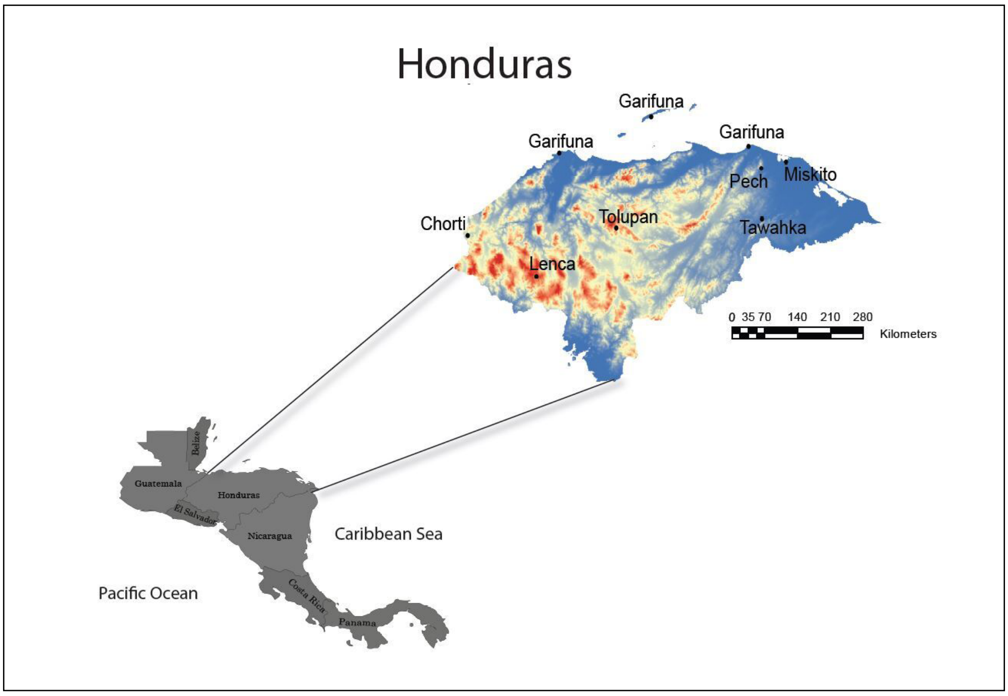

**FIGURE 1.** Map of Central America showing the location of the Honduran indigenous and Garifuna populations mentioned in the text.

From a demographic perspective, Honduras, like most Latin American nations, is characterized by a diverse population with varying proportions of European, African, and indigenous (Amerindian) genetic ancestry, especially evident in urban centers (Herrera-Paz, 2019; Norris *et al*., 2018). Currently, a significant portion of the Honduran population is concentrated in the departments of Cortés and Francisco Morazán, which encompass the country's primary cities and urban hubs known for high rates of positive migration (Herrera-Paz *et al*., 2014; Herrera-Paz, 2013a).

The ethnic composition of Honduras is an intricate mosaic comprising eight distinct groups, many of which remain highly isolated in rural areas and together account for approximately 7% of the nation's total population (https://ine.gob.hn/v4/). This diversity includes five indigenous American populations: Lenca, Maya-Chortí, Tawhaka, Pech, and Tolupán (or Xicaque). Additionally, there are two groups with significant African Ancestry and Indigenous American heritage: the Garifuna and the Miskito (Hasseman *et al*., 2017; Offen, 2002).

These seven populations are distributed across three main geographic regions: the Caribbean coastal area, the western/central highlands, and the tropical rainforest region known as "The Moskitia or Mosquitia", which spans eastern Honduras and western Nicaragua. The western highlands are home to the Chortí, Lenca, and Tolupán, with the latter concentrated in the Montaña de la Flor. The Tawahka, Pech, and Miskito inhabit the forests and coastal areas of La Mosquitia, while the Garifuna are dispersed along the Caribbean coast in over 50 communities. This distribution underscores the diverse cultural and environmental contexts that have shaped the histories and lifestyles of these Indigenous groups.

## The Garifuna

The Garifuna people have been a focal point of genetic research in Honduras, with numerous studies contributing to the understanding of their history (Beaty, 2017; Beaty *et al*., 2017; Crawford, 1983a, 1983b; Herrera-Paz, 2017; Herrera-Paz *et al*., 2008, 2010; Phillips-Krawczak, 2012). Comprehensive insights into the origins and history of the Garifuna are found in Crawford (1983a, 2024) and De Andrade Coelho (1993).

Briefly, during the 16th century, the island of St. Vincent in the Lesser Antilles was inhabited by Indigenous groups that emerged from the intermingling of Arawak and Carib Amerindians, collectively known as the Red Caribs. The arrival of escaped Africans who had avoided enslavement, and integrated with the Red Caribs, led to the formation of a new, mixed population: the Black Caribs, later known as the Garifuna. This group preserved African cultural elements while incorporating the language and agricultural practices of South American indigenous peoples, notably fishing and cassava (*Manihot* sp.) cultivation.

Following conflicts with the English over control of St. Vincent Island, in 1797, approximately 2,026 Garifuna were forcibly deported to Roatan Island off the Honduran Caribbean coast. Shortly after, a portion of the group was relocated by the Spaniards to the city of Trujillo on the Caribbean continental coast of Honduras. In Roatan, the Garifuna founded the community of Punta Gorda, while in Trujillo, they established the settlements of Cristales and Río Negro. From these initial locations, they expanded eastward and westward, along the Honduran Caribbean coast. The Garifuna also founded communities along the Caribbean coasts of Guatemala, Belize, and Nicaragua, and later established significant populations in major US cities. These communities trace their origins back to the initial migration from St. Vincent (Crawford, 1983b).

Today, the Garifuna population numbers approximately 300,000 individuals (Williams, 2014). Their exceptionally high fertility rates have led to a 200-fold population increase over a span of just two centuries, representing a unique and noteworthy example of biocultural adaptation, as noted by Crawford (1983b).

The admixture of African and Amerindian genetic lineages, along with the impact of founder effects, adds depth to the study of the Garifuna. Additionally, their unique cultural syncretism, combined with high fertility and migration rates, positions them as an intriguing subject for research within biological anthropology.

## Maya-Chortí

The Chortí, or Ch'orti', are an Indigenous group historically inhabiting areas of present-day Guatemala, Honduras, and El Salvador (Metz, 2016).

Historical records date back to 1530, when Spanish military forces led by Pedro de Alvarado conquered Chortí villages near what are now the ruins of Copán. By the 18th century, the Chortí territory had been divided by the political boundaries of Guatemala, Honduras, and El Salvador. During this period, approximately 40,000 Chortí people lived in the department of Ocotepeque and in various municipalities of the department of Copán, including the Copán Ruinas. According to the 2001 national census, the Chortí population in Honduras was spread across fifty-six villages or *aldeas* (Davidson, 2011). Acosta (2010) notes that the Chortí are the second-largest ethnic group in western Honduras and the fourth-largest nationwide.

The Chortí language is part of the Mayan linguistic family, closely related to Cholanan and Classical Maya languages (Houston *et al*., 2001). Although the language has largely disappeared in Honduras, speakers remain in areas near the Guatemalan border (Herranz, 2000). Due to assimilation and educational policies, contemporary Chortí people primarily speak Spanish.

## Lenca

The Lenca are the most populous American Indigenous group in Honduras, predominantly residing in the southwestern part of the country, particularly in the departments of Lempira, Intibucá, and La Paz. Their territory also extends into neighboring regions of El Salvador. According to the most recent Honduran census (XVII Population Census and VI Housing Census) conducted in 2013, 453,670 individuals self-identified as Lenca (Gobierno de Honduras, 2015), representing 5.24% of the total Honduran population (Valle *et al*., 2018). The Lenca population is concentrated primarily in the departments of Lempira (33.6%), Intibucá (26.7%), and La Plaz (24.1%), collectively encompassing 84.4% of the entire Lenca population.

The linguistic history of the Lenca remains an area of scholarly debate. While some linguists argue for potential connections to the Mixe-Zoque, Xinca, or even Mayan languages, Constenla Umaña (1991) suggests that the Lenca language might be related to the Misumalpa and Chibchan languages. Given the presence of all three linguistic families (Lenca, Misumalpa, and Chibcha) in Honduras, Constenla Umaña (2002) proposes that this region may have been the original settlement of the proto-Lenmichí speakers, who later dispersed southward.

## Tolupan

Also known as Jicaques or Xicaques, the Tolupán currently inhabit the departments of Olancho, Yoro, and Atlántida, with a significant population located in the Montaña de la Flor in Francisco Morazán. During the 16th and 17th centuries, Spanish colonizers forced the Tolupán to abandon their ancestral lands along the Caribbean coast, prompting them to seek refuge in the forests and mountains of central and northern Honduras (Chapman, 2007). In response to this displacement, the Tolupán adapted to a more sedentary lifestyle, relying on subsistence agriculture.

The origins of the Tolupán language have been a subject of ongoing linguistic debate. While some scholars propose a Mesoamerican origin for the language, others, such as Greenberg and Swadesh (1953), have suggested a connection to the Hokan-Sioux family. This view contrasts with the perspective that Tolupán is an independent, isolated language. Despite these differing opinions, the consensus among linguists, as proposed by Campbell and Oltrogge (1980), is that the Tolupán language is most closely related to the Jicaque-Tol linguistic family.

## Tawahka

The Tawahka are an Indigenous group located in the remote regions of the Honduran Mosquitia and Nicaragua, primarily along the Patuca and Wampú rivers. According to the 2013 population census in Honduras, the Tawahka population numbers around 2,692 individuals (Gobierno de Honduras, 2015). Although Herrans (2000) distinguishes between the Mayangna-Sumu of Nicaragua and the Tawahka of Honduras as separate groups, they are considered to share a common ethnic origin, despite these self-identified distinctions.

The Tawahka language, known as Sumo or Mayangna, belongs to the Misumalpa linguistic family (Constenla Umaña, 2002, 2005). According to Salamanca (2007), there are currently approximately five hundred speakers of Sumo-Tawahka in Central America.

Due to their small population size and geographical isolation, the Tawahka have faced significant demographic challenges throughout their history. Between the 1830s and the period from the 1920s to the 1940s, they experienced substantial population declines, primarily caused by the introduction of infectious diseases such as measles and influenza, which had devastating effects on their communities (McSweeney, 2002). This population decline was so severe that it resulted in a demographic bottleneck event. McSweeney also notes that the Tawahka population is relatively young, with an average of 16 years, and three-quarters of the population are under the age of 24. In the 1990s, there was a notable increase in the birth rate, with approximately fifty-six births per 1,000 inhabitants.

The Tawahka traditionally organize themselves in small, scattered settlements along the rivers. This dispersed settlement pattern has allowed them to maintain their traditional subsistence practices, which rely heavily on fishing, hunting, and small-scale agriculture (Suárez, 2002).

Additionally, the Tawahka's isolated geographic location significantly limits their access to medical services, resulting in a high rate of infant mortality within the population. Remarkably, the Tawahka are considered one of the least genetically admixed groups in Central America (McSweeney, 2002). However, our fieldwork conducted in the community of Krausirpe has documented a substantial influx of Miskito immigrants who have intermarried with the Tawahka people, leading to increased genetic admixture in this community.

## Pech

The Pech, an Indigenous people native to the eastern regions of Honduras, primarily inhabit the eastern departments of Olancho, Colón, and Gracias a Dios. According to the most recent national census conducted in 2013, the Pech population totals 6,023 individuals, with the majority (61.15%) residing in the department of Olancho (Gobierno de Honduras, 2015). This marks a significant increase from the 2001 census, which recorded 3,141 Pech individuals within their Indigenous territories, covering an area of 112,492 km$^2$ (Vargas Aguilar, 2006).

Linguistic studies suggest that the Pech may have migrated from South America to their current location, with the eastern region of Olancho believed to be their ancestral settlement area (Constenla Umaña, 1989). However, the origins of the Pech remain unclear due to the limited scientific research, particularly in archaeology and population genetics (Vargas Aguilar, 2006).

The Pech language, also known as Paya, belongs to the Chibchan linguistic family, a diverse group of languages spoken from eastern Honduras to northern Colombia. As the northernmost language in this family, Pech is of particular importance to linguists studying the historical distribution and relationships among Chibchan languages. Constenla Umaña (1991) suggests that Pech is more closely related to the Misumalpa languages (Ulua, Sumo, Miskito, and Cacaopera) than to the core Chibchan languages. Within the Chibchan family, it shows stronger similarities to the Rama and Guatuso languages of Costa Rica. Despite its linguistic significance, Pech remains one of the most poorly documented living Chibchan languages, alongside Chimila and Bari from Colombia (Constenla Umaña, 1993).

The Pech have traditionally relied on a subsistence economy based on fishing, hunting, and agriculture. Maize is their primary staple crop, while they also cultivate a variety of tubers, such as cassava and yams, which diversify their diet and enhance agricultural resilience (Vargas Aguilar, 2006).

## Miskito

The Miskito are an ethnic group that inhabits the Mosquito Coast in the Caribbean, particularly along the riverbanks of the Mosquitia region. Their traditional territory stretches from Cabo Camarón in Honduras to Río Grande de Matagalpa in Nicaragua. In Honduras, the Miskito population is estimated to be close to 80,000 individuals (Gobierno de Honduras, 2015).

Originally, the Miskito were a small community located near Cape Gracias a Dios. From the 17th to mid-19th centuries, the English exerted influence over the Mosquitia region, exploiting its resources and exercising authority through the Miskito Kings, who ruled over the territory from the Tinto (Negro) River to the San Juan River in Nicaragua. This prolonged period of interaction and intermixing with English colonizers and African populations played a crucial role in shaping the genetic and cultural identity of the present-day Miskito people (Conzemius, 1929; Dennis, 1985; Helms, 1983; Herlihy, 2002).

The Miskito have a significant presence along the Caribbean coast of Honduras and Nicaragua, particularly in the Honduran Mosquitia region. Their language, also known as Miskito or Miskitu, belongs to the Misumalpan language family, which also includes other Indigenous languages of the region, such as Sumo and Mayangna (Hasseman *et al*., 2017). This linguistic affiliation highlights the shared cultural and historical connections between these Indigenous groups in the region.

Biologically, the contemporary Miskito population is a genetically admixed group, shaped by the intermingling of Indigenous peoples, Africans, and European immigrants throughout history. Studies conducted among the Miskito in Nicaragua have revealed a significant proportion of polymorphic loci, indicating a diverse ancestral background. Azofeifa *et al*. (1998) highlighted the remarkable genetic diversity within the Miskito gene pool. Further supporting these findings, Morera-Brenes (2006) estimated that the genetic admixture of the Nicaraguan Miskito is trihybrid, comprising European, Amerindian, and African ancestral components. Given the shared historical and cultural connections between the Miskito populations of Nicaragua and Honduras, it is likely that similar patterns of genetic admixture and diversity would be observed in the Honduran Miskito, should they undergo comprehensive genomic analysis.

Traditionally, the Miskito have engaged in a diverse range of subsistence activities, including fishing, hunting, and agriculture. Due to their coastal location, marine resources are particularly important to both their economy and culture. The Miskito are skilled fishers, employing a variety of techniques to harvest fish, lobsters, and other seafood, which play a central role in their livelihood (Herlihy, 2012).

## ANTHROPOLOGICAL GENETICS RESEARCH IN HONDURAS

### Ongoing research

In the context of Honduras, there exists a notable in prior bioanthropological investigations on Indigenous populations, Afro-descendant communities (beyond the work of Herrera-Paz & Crawford), and local mestizo groups. Specifically, these populations have not been subjected to comprehensive *in situ* population genetic analyses, which would involve rigorous fieldwork examining the distribution of biomarkers. Apart from the Garifuna, most of the Indigenous populations in Honduras have not been studied since the early blood polymorphisms and anthropometric investigations conducted between the

1930s and 1960s (D´Aloja, 1939; Matson & Swanson, 1963). This lack of contemporary, in-depth, and localized research has hindered our understanding of the evolutionary history of these groups, and the potential health implications linked to their distinct genetic backgrounds.

To address this knowledge gap, a multidisciplinary research team, comprising institutions such as the University of Costa Rica, University of Kansas, Catholic University of Honduras, the Consortium on Asthma among African-ancestry Populations in the Americas (CAAPA), and the University of Tasmania, has undertaken extensive fieldwork and produced some scholarly contributions. Preliminary research insights are currently undergoing analysis for peer review and publication. These findings are the result of fieldwork conducted between 2013 and 2019 among Indigenous communities in Honduras, which enabled the collection of biological samples (e.g., DNA, anthropometric data, diet, and microbiome) while adhering to strict ethical protocols and respecting cultural sensitivities. In parallel, ethnographic data have also been gathered to provide context for the genetic findings within these Indigenous groups.

One of the authors, Edwin Francisco Herrera-Paz (EFHP), a faculty member at the *Universidad Católica de Honduras* (UNICAH) School of Medicine, became a member of the Consortium on Asthma among African-ancestry Populations in the Americas (CAAPA). This consortium, formed by several academic institutions in the United States and other countries in the Americas and Africa, aims to investigate the genetics of bronchial asthma in populations of African ancestry. The CAAPA arm in Honduras, known as Honduras Asthma (HONDAS), required sampling more than 1,000 asthma cases and healthy controls from 12 Garifuna communities along the Honduran Caribbean coast for genetic and genomic analyses. (For more information on CAAPA, visit: https://www.ncbi.nlm.nih.gov/projects/gap/cgi-bin/study.cgi?study_id=phs001123.v2.p1).

In 2015, Norberto F. Baldi (NFB), a biological anthropologist with a PhD from the University of Kansas and faculty member at the Universidad de Costa Rica, joined the fieldwork to collect samples for mitochondrial and Y chromosome analyses. The following year, NFB secured a grant from National Geographic's Genographic Project 2.0 to study the distribution and extent of the Chibchan-speaking populations in Central America, with a focus on Honduras.

The synergy of our collaborative international efforts led to the collection of samples from communities representing the six Indigenous populations of Honduras described above. These samples were subsequently genotyped using the GenoChip array (Elhaik *et al*., 2013). By integrating SNP data from both genetic microarrays and whole genome sequencing, will aim to create a comprehensive genetic profile of Honduran Indigenous populations. This integrated approach holds significant potential for advancing our understanding of population health and historical demography.

In our research, we obtained informed consent from each participant in accordance with the approval granted by the ethics committee of UNICAH. During the collection of biological samples, we also provided basic medical and dental services, including examinations, cleanings, minor treatments, and medical consultations. These services not only benefited the participants but also contributed valuable data for our study. Furthermore, as part of our ethical commitment and social responsibility, we aim to return to the same communities to deliver the results of our research.

By directly engaging with the Indigenous populations of Honduras, our research team aims to address critical knowledge gaps and enhance understanding of the genetic diversity, history, and adaptations of these often understudied populations. Through this work, we seek to generate significant scientific findings while upholding ethical standards that promote responsible scientific field practices. Our approach prioritizes collaboration, ensuring that the research process is respectful and beneficial to the communities involved.

## Bioanthropological research on the Garifuna

The genetic structure and demographic history of the Garifuna have been approximated using various methods, such as the distribution of genetic and biochemical markers, migration matrices, and even surname distribution analysis. In fieldwork conducted in 2000, samples were collected from three Garifuna communities along the Honduran Caribbean coast to assess allele and genotype frequencies of thirteen forensic DNA microsatellites (CODIS STR *loci*). These *loci* are commonly used in human identification and paternity testing (Herrera-Paz *et al*., 2008). The specific *loci* can be found at the FBI CODIS Core STR Loci website (https://strbase-archive.nist.gov/fbicore.htm). While reference population sampling with forensic markers is essential for establishing probabilities in forensic and paternity cases, these markers also provide insights into recent demographic history and genetic distances (Herrera-Paz, 2019).

Questionnaires included questions about the places of birth and residence of the sampled individuals, their parents, and grandparents. The data collected through these questionnaires enabled the construction of migration matrices, which revealed differential gender-based migration patterns across two ancestral generations. While neolocality (establishing a new residence) predominated in the grandparental generation, indicating a peopling pattern along the coast, a matrilocal residence pattern with significant male mobility between communities was observed in the parental generation. Furthermore, the matrices highlighted a high rate of male migration to Garifuna communities near cities, which are known developmental hubs in Honduras. Phylogenetic trees constructed using allelic frequencies revealed a genetic relationship between the Garifuna and other Afro-Caribbean and African groups (Herrera-Paz *et al*., 2010). Additionally, surname frequency data were collected from the Honduran National Registry databases for several Garifuna communities. These data, analyzed using isonymy techniques, were instrumental in assessing genetic relationships among the communities, thereby shedding light on peopling and migration patterns (Herrera-Paz, 2013b).

The elucidation of migratory patterns and residence customs is crucial not only to anthropology but also to epidemiology. This is because the transmission and dispersion patterns of certain pathogens, such as *Helicobacter pylori* and HIV, often align to human migration patterns (Gandhi *et al*., 2015; Herrera-Paz, 2013c).

Whole-genome sequencing was conducted by CAAPA on samples from approximately 1,000 individuals of African ancestry residing in various locations across the United States and the Americas, including fifty Garifuna individuals. The study aimed to capture the genetic variability of the African diaspora across the Americas. Mathias *et al*. (2016) documented the genomic diversity within these populations, as well as the genetic distances among them, shaped by the legacy of the African slave trade and the varying proportions of admixture with Indigenous American and European ancestries.

In an alliance with CAAPA, industry partners, and other consortia (https://www.illumina.com/science/consortia/human-consortia/multi-ethnic-genotyping-consortium.html), SNPs data collected in the WGS study were used to develop DNA chips (Johnston *et al*., 2017). These chips are commonly used in Genome-Wide Association Studies (GWAS) to identify contributing *loci* in multifactorial diseases. A GWAS performed by CAAPA on asthma cases and controls from African-ancestry individuals across the Americas, which included more than 300 Garifuna samples collected in several communities during our fieldwork, identified both known and novel SNP *loci* involved in asthma susceptibility. One of these novel asthma-related loci was located in the *17q12–q21* region (Daya *et al*., 2019). Analysis of SNP data from the GWAS study to assess microevolution and local ancestry in the Garifuna population are ongoing.

Finally, the WGS data generated through this research have contributed to the construction of the first human pangenome, the African pangenome, a comprehensive catalog of genetic variation across multiple African populations (Sherman *et al*., 2019). Notably, the African pangenome revealed nearly three hundred megabase pairs (Mbp) of genetic material not reported in the reference human genome. This additional genetic content, which accounts for 10% of the genome and is predominantly composed of structural variation, suggests that human genomic diversity is more extensive than previously recognized.

## Evidence of a strong founder effect in Honduran Garifuna

The history of the Honduran Garifuna population is marked by two genetic bottlenecks: the first occurred after the shipwreck near Saint Vincent, and the second took place during their deportation to Honduras. Founder effects, which occur following such population bottlenecks, are known to leave distinct signatures in the distribution of biological markers. Specifically, a founder effect often results in a reduction of allele diversity, particularly for those that occur at low frequencies in the original population (Maruyama & Fuerst, 1985).

As a result, populations may exhibit lower expected heterozygosity, and a reduction in singletons and doubletons (i.e., genetic variants seen just once or twice in the population). Additionally, founder effects can lead to high differentiation between the current population and its ancestral group.

Mathias *et al*. (2016) identified a founder effect in the Garifuna population through an analysis of 113,090 SNP markers derived from the CAAPA whole genome sequences, encompassing sixteen populations. Thirteen of these represented African-ancestry populations across the Americas, including the Garifuna, while the remaining three were the hypothesized ancestral populations: African, European, and Native American. Principal Component Analysis (PCA) was employed to investigate continental ancestry and genetic distances, revealing that the Garifuna clustered primarily with African populations in the first two principal components (PC1 and PC2), but displayed clear differentiation in the third component (PC3). Among the analyzed groups, the Garifuna stood out as the only populations exhibiting such significant divergence from the African genetic pool. This differentiation in PC3 could not be attributed to local admixture with mestizo or Indigenous American groups, as varying levels of tri-continental admixture were already reflected in PC1 and PC2.

Mathias *et al*. (2016) further examined genetic relatedness among groups based on the number of doubletons shared by pairs of populations. The resulting heat maps from this pairwise analysis indicated a pronounced differentiation of the Garifuna from other populations of African ancestry, supporting the hypothesis of a significant genetic bottleneck. This analysis underscores the unique genetic signature of the Garifuna, shaped by historical events and founder effects, contributing to their distinct position among Afro-descendant populations in the Americas.

Founder effects, such as those experienced by the Garifuna, often lead to abrupt changes in allelic frequencies compared to the source population, potentially including medically significant variants. This shift can alter the epidemiological profile of the population. Notably, bronchial asthma is particularly prevalent among Garifuna communities and has been linked to both genetic susceptibility and co-infections, such as infestation by the intestinal nematode *Ascaris lumbricoides* (Herrera-Paz, 2017; Santos-Fernández *et al*., 2016). These findings emphasize how genetic and environmental interactions can shape health outcomes within specific populations.

Hypertrophic cardiomyopathy (HCM) is a complex, heterogeneous autosomal dominant disorder caused by mutations in sarcomere genes. This condition can manifest in various ways, including heart failure, cardiac ischemia, and sudden death (Glavaški *et al*., 2023). Notably, previous research identified an HCM-associated missense mutation in the sarcomere protein *MYBPC3* among Garifuna patients with left ventricular hypertrophy living in New York City. This discovery underscores the potential impact of founder effects and genetic drift on the prevalence of specific cardiomyopathic mutations within the Garifuna population, reflecting their unique genetic history and the influence of past bottlenecks on current health risks.

In a genetic study, individuals from various Garifuna communities in Honduras, an allele associated with Hypertrophic Cardiomyopathy (HCM) was found at frequencies as high as 4.7% in some communities (ongoing work). This is notably high for an autosomal dominant allele, as such variants with significant disease penetrance are generally subject to purifying selection that reduces their frequency in a population. The most plausible explanation for this unexpectedly high prevalence is a founder effect, where a small initial population size leads to the proliferation of specific genetic traits.

Given the substantial public health implications posed by the widespread presence of a genetic variant linked to cardiac illness, a larger-scale study is being planned in collaboration with the Honduran government. This comprehensive screening initiative aims to encompass the entire Garifuna population. By doing so, it will yield a more thorough understanding of the distribution and clinical significance of the HCM-linked allele within this distinct Afro-Indigenous group. The findings will help inform targeted health interventions and guide public health policies to manage and mitigate the impact of Hypertrophic Cardiomyopathy in the Garifuna communities.

## Tri-continental proportions of admixture in Honduran Garifuna

Percentages of genetic contributions from tricontinental parental populations to the Garifuna have been extensively studied using various genetic markers. Crawford *et al*. (1981), analyzed blood groups and polymorphic enzymes in a Garifuna community from Livingston, Guatemala, and found an African genetic contribution ranging between 70.0%–75.2%, and Indigenous American component between 22.4%–29.0%, and a minor European influence ranging from 1.0%–2.4%. This early work highlights the complex ancestry of the Garifuna, rooted in the historical admixture of African, Indigenous American, and European populations, with a predominantly African heritage that aligns with the historical and cultural narratives of this Afro-Indigenous group.

Mathias *et al*. (2016), analyzing WGS SNP data from forty-two Honduran Garifuna individuals, reported genetic contributions of 81.0% African, 17.0% Indigenous American, and 2.0% European ancestry. This finding stands out when compared to the fifteen other African-ancestry populations across the Americas included in the study, which displayed significant European genetic contributions. The Garifuna from Honduras, however, exhibited an exceptionally low European ancestral component. This contrasts with findings from Benn Torres *et al*. (2019), which noted that Garifuna populations from Saint Vincent Island had higher proportions of European ancestry. These variations underscore the complex demographic histories and unique genetic legacies among Garifuna communities across different regions. The lower European genetic ancestry observed in Honduran Garifuna, as opposed to those from Saint Vincent, may be partly explained by the selective deportation of darker-skinned Garifuna by the English, which could have reduced the European genetic input in the Honduran population. However, Crawford (personal communication) recommends approaching this interpretation with caution, emphasizing the inherent complexities involved in sampling admixed populations across different geographic regions. Such complexities can introduce variability in ancestry estimates and highlight the importance of considering historical, social, and sampling context when interpreting genetic data.

## Further evidence of a bottleneck

To evaluate the genetic relationships of the Garifuna population in comparison with other populations from the Americas, Europe, and Africa, and to identify further evidence of the founder effect, we conducted a Principal Component Analysis (PCA) using allelic frequencies from thirteen STR markers. These *loci* form the core set used in the original CODIS list, which is a standard in forensic genetics and paternity testing. The markers analyzed were *CSF1PO, FGA, TH01, TPOX, VWA, D3S1358, D5S818, D7S820, D8S1179, D13S317, D16S539, D18S51*, and *D21S11* (source: FBI CODIS Loci, https://www.fbi.gov).

Allelic frequencies for three Garifuna communities in Honduras were extracted from Herrera-Paz *et al*. (2008). For comparative analysis, allelic frequencies from other populations were obtained from references cited in Herrera-Paz *et al.* (2010), previously used for constructing phylogenetic trees. All data were organized into an Excel spreadsheet for comprehensive comparison, and PCA analysis was conducted using the "Multibase" software (available at https://pkg.go.dev/github.com/multiformats/go-multibase). This approach enabled the investigation of genetic relationships and variation patterns among the Garifuna and comparative populations across the Americas, Europe, and Africa. The PCA plots generated provide insights into both global and local ancestries, serving as a complementary tool to the phylogenetic trees found in Herrera-Paz *et al.* (2010).

The principal component analysis (PCA) plot, shown in Figure 2, visually illustrates the genetic relationships among the analyzed populations. Each data point in the plot corresponds to an individual population, and the colors indicate their broader continental groups. In the PC1 dimension, the Garifuna are observed to cluster closely with other Afro-Caribbean and African populations, underscoring the strong African genetic component within the Garifuna population. This clustering aligns with previous findings of the Garifuna's predominant African ancestry, and highlights the genetic signature shaped by their African roots, particularly from the transatlantic slave trade.

However, the Garifuna notably deviates from this overall pattern when examining the PC2 and PC3 components. This divergence can be attributed to the strong founder effect experienced by the Garifuna, further reinforcing the genetic consequences of the historical bottleneck, as reported in literature using SNPs, forensic STRs, and mitochondrial markers. In summary, these effects include increased expected homozygosity and high *Fis* values, a reduction in the number of low-frequency variants, and significant differentiation from the source populations (Herrera-Paz, 2017; Herrera-Paz *et al.*, 2008, 2010; Mathias *et al.*, 2016; Salas *et al.*, 2005).

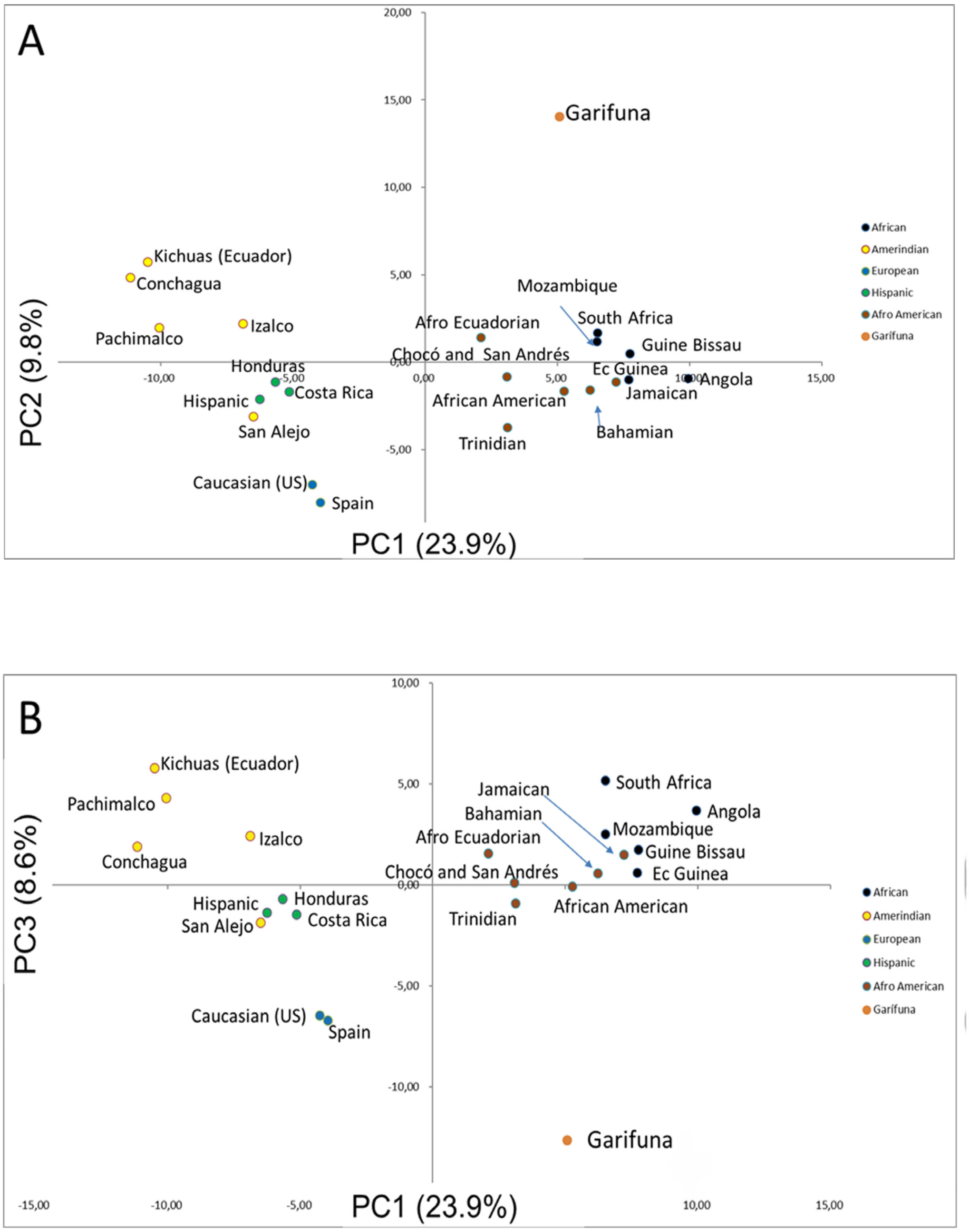

**FIGURE 2.** MPCA analysis of 22 populations using 13 autosomal STR allelic frequencies, commonly used in forensic applications. **A:** PC1 vs. PC2; **B:** PC1 vs. PC3. Populations: American Indigenous: **1.** Kichuas (Ecuador), **2.** Conchagua (El Salvador), **3.** Pachimalco (El Salvador), **4.** Izalco (El Salvador), **5.** San Alejo (El Salvador). Hispanic: **6.** Hispanic (U.S.), **7.** Honduras (general population), **8.** Costa Rica (general population). European: **9.** Caucasian (U.S.), **10.** Spain. Afrodescendants from the Americas: **11.** Afro-Ecuadorian (Ecuador), **12.** Afro-Colombian (Colombia), **13.** Trinidad (U.S.), **14.** African American (U.S.), **15.** Bahamian (from U.S.), **16.** Jamaican (U.S.), African: **17.** South African, **18.** Mozambique, **19.** Guiné Bissau, **20.** Equatorial Guinea, **21.** Angola, and **22.** Garifuna from Honduras. Allelic frequencies for the Garifuna population (22) are found in Herrera-Paz (2017); Herrera-Paz *et al.*, (2008, 2010). Frequencies for other populations were taken from González-Andrade *et al.* (2006) [1, 11]; Lovo-Gómez *et al.* (2007) [2-5]; Budowle *et al.* (1999) [6, 9, 13-16]; Matamoros *et al.* (2008) [7]; Rodríguez *et al.* (2007) [8]; Camacho *et al.* (2007) [10]; Paredes *et al.* (2003) [12]; Kido *et al.* (2007) [17]; Alves *et al.* (2004, 2005) [18, 20]; Gonçalves *et al.*, (2002) [19]; and Beleza *et al.* (2004) [21].

## CONCLUDING REMARKS

Anthropological genetics has made significant progress in understanding human diversity and the evolutionary history of populations. In this context, the study of Honduran Indigenous populations has gained relevance due to their geographical location, cultural diversity, and relative isolation. Since the 1990s, efforts have been made to clarify the genetic relationships among populations in southern Central America. However, Honduras remains one of the countries where Indigenous populations have been least studied by biological anthropologists (Baldi & Barrantes, 2019).

Honduran Indigenous populations are distributed across two cultural areas: the Mesoamerican and the Isthmo-Colombian, which correspond to distinct geographical regions and ecosystems (Bergoeing, 2015; Hoopes & Fonseca, 2003; Redo *et al*., 2009; Richard *et al*., 1963). This geographical, cultural, and linguistic separation has significantly shaped their ways of life and social organization, potentially influencing their genetic structure.

The Chortí and Lenca populations of the western Honduran region have experienced a more accelerated process of admixture, acculturation, and assimilation into the national culture compared to the Pech, Tawahka, or Miskito populations, which reside in the forested and remote areas of La Mosquitia.

This cultural and geographical diversity makes the study of Honduran Indigenous populations particularly valuable, offering unique insights into the historical and evolutionary processes that have shaped human diversity in the country.

Furthermore, small and isolated populations present a unique opportunity for genetic research. These populations may have experienced distinct evolutionary pressures, including environmental adaptations and cultural practices, which have shaped their genetic composition. Analyzing genetic variation in such groups can provide valuable insights into their demographic history, including population bottlenecks, expansions, and migrations (Cox *et al*., 2016; Kristiansson *et al*., 2008; Nair & Baier, 2015; Pardo *et al*., 2005; Sheffield *et al*., 1998). Our studies will contribute to a more comprehensive understanding of the evolutionary history of Honduran populations within the broader Central American context.

Additionally, studying these populations has significant implications for health and disease research. The genetic structure of small and isolated groups can lead to higher frequencies of rare genetic disorders or disease susceptibility alleles due to founder effects or genetic drift. This phenomenon is exemplified by the high incidence of asthma and hypertrophic cardiomyopathy among the Garifuna. Such findings not only contribute to our understanding of population-specific health risks but also offer valuable insights into the genetic basis of these conditions in broader populations.

The genetic characterization of these Garifuna and other populations also has important implications for biomedical research and personalized medicine. By identifying population-specific genetic variants associated with disease susceptibility or drug response, healthcare strategies can be tailored to the unique genetic backgrounds of these communities, leading to more effective and targeted treatments.

Finally, we anticipate that our research in Honduras will serve as a crucial link between contemporary genetic data and ancient DNA studies. By comparing the genetic profiles of current indigenous populations in Honduras with ancient DNA samples from archaeological sites in the region, we aim to create more accurate reconstructions of historical population parameters. These comparisons are expected to allow for the estimation of critical demographic shifts, such as population bottlenecks, expansions, or replacements,

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that may have occurred over time. Such analyses will contribute to a more nuanced understanding of long-term population dynamics in Central America and provide insights into how these dynamics have shaped genetic diversity in the region.

## CONFLICT OF INTEREST

There is no conflict of interest.

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