Exchanging fluids

The sociocultural implications of microbial, cultural, and ethnic admixture in Latin America

Tomás Cabeza de Baca ⓘD, *University of Arizona*

Aurelio José Figueredo, *University of Arizona*

Heitor Fernandes, *University of Arizona*

Vanessa Smith-Castro, *Universidad de Costa Rica*

ABSTRACT. **Knowledge of evolutionary influences on patterns of human mating, social interactions, and differential health is increasing, yet these insights have rarely been applied to historical analyses of human population dynamics. The genetic and evolutionary forces behind biases in interethnic mating and in the health of individuals of different ethnic groups in Latin America and the Caribbean since the European colonization of America are still largely ignored. We discuss how historical and contemporary sociocultural interactions and practices are strongly influenced by population-level evolutionary forces. Specifically, we discuss the historical implications of functional (de facto) polygyny, sex-biased admixture, and assortative mating in Latin America. We propose that these three evolutionary mechanisms influenced mating patterns, shaping the genetic and cultural landscape across Latin America and the Caribbean. Further, we discuss how genetic differences between the original populations that migrated at different times into Latin America contributed to their accommodation to and survival in the different local ecologies and interethnic interactions. Relevant medical and social implications follow from the genetic and cultural changes reviewed.**

Key words: Latin America, Genetic Admixture, Evolutionary Anthropology, Assortative Mating, Pathogen Resistance, Dutton's Rule

For the purpose of explaining our theoretical argument succinctly and with utmost clarity, we first state the major goals of this study as simply as possible, without derailing the narrative to provide the needed documentation or empirical support for any of the assertions that follow. We then provide the evidentiary bases for these claims, which will be elaborated in the following sections.

The purpose of this article is to explore the proposition that the typical Latin American of the present era is a product of protracted interethnic hybridization between European and Amerindian (*mestizo/a*), between European and African (*mulatto/a*), or between all three (*pardo/a*), plus up to 500 years of subsequent gene-

culture coevolution that selected among the combinations of ancestral genes to favor the genotypes that were best adapted to the novel conditions produced by the Columbian Exchange. Gene-culture coevolution goes beyond either pure genetic or pure cultural evolution in that it also encompasses the various interactions among genetic and cultural factors: (1) genetic factors may bias the socially mediated learning of cultural traits by means of naturally selected epigenetic rules of development; and (2) cultural factors may bias genetic transmission by influencing the social environment in which genetic selection takes place (Lumsden & Wilson, 1981; Richerson & Boyd, 2005).

Jablonka and Lamb (2005) identified four dimensions of inheritance on which selection might be considered to act: (1) genetic variation, (2) epigenetic variation, (3) behavioral variation, and (4) symbolic variation. Gene-culture coevolution involves all of these processes, but most prominently it features the interaction of

genetic with symbolic variation. Thus, we maintain that interethnic hybridization was sexually asymmetrical from the outset, favoring pairings of European males with either Amerindian or African females. This asymmetry is attributable to the sociohistorical conditions of the European (specifically, Iberian or Lusitano-Hispanic) conquest of most of Central and South America, as well as the Caribbean. As conquerors frequently do, the Spanish and Portuguese set themselves up at the upper echelons of the social hierarchy in their American colonies, most notably with respect to the enslaved people at the bottom. This gave the male colonizers preferential access to the colonized females by means of physical force, social pressure, or voluntary hypergamy. The prevailing sociohistorical conditions therefore influenced the relative population frequencies of European Y chromosomes and Native American or African mitochondrial DNA (mtDNA), as we will discuss later in the article. This can be interpreted as the influence of ecocultural (behavioral and symbolic) variation on genetic variation. Likewise, the subsequent selection among the newly created European-Amerindian and European-African hybrids was shaped by both biological and sociocultural forces.

The biological forces included the exchange of parasites between what were previously somewhat geographically isolated populations, resulting in a cross-contaminated pool of pathogens to which none of the three ancestral populations were adapted. This novel biological community of human parasites posed an adaptive challenge that would define the selective pressures faced by the newly created populations of hybrids as well as the ancestral populations that remained. The sociocultural forces included the social stratification of the hybrid populations according to the proportion of European ancestry possessed, with those of higher European ancestry occupying positions that were higher in the social, political, and economic hierarchies.

When genetic hybrids are created by sexual means, many different combinations of the two parental genotypes appear among the offspring, and these hybrid genotypes may differ substantially in fitness. Thus, in natural environments, hybridization is nearly always followed by selection among the alternative combinations of alleles. If no selective pressures favored certain combinations over others, then evolution would, quite simply, not occur. However, if novel selective pressures arose as result of the contact between the ancestral populations, then evolutionary processes would

inevitably shape the hybrid population to adapt it to the postcontact ecology.

Thus, many factors must be considered when delineating the roots of humans and the migration of genes in relation to the effects of mating patterns on population parameters. Extra considerations must be made when investigating populations with a history of genetic admixture, or genetic mixing of two or more populations. According to Jobling and colleagues (2013, p. 447), when investigating genetic admixture, "genetics cannot be divorced from . . . sociological considerations, since they directly influence the nature of the admixture." Thus, we attempt to "think anthropologically about genetics" (Algee-Hewitt & Goldberg, 2016, p. 557) but also *genetically about history*. Latin America is a perfect example of a society influenced culturally, socially, and genetically by the admixture of distinct populations—mainly, European migrants, Amerindians, and African slaves (Skidmore & Smith, 2005; Smith, 1997).

The legacy and history of Latin America and the Caribbean have been described by some scholars as "born of blood and fire" (Chasteen, 2004, p. 15), highlighting the conflictual and violent catastrophes that swept through the Americas, selecting against less adaptive individuals, and eventually producing a society of people endowed with grit and resiliency to adapt and overcome such conflict. For example, Mexican psychologist Rogelio Díaz-Guerrero (2014, p. xx), in his foreword, stated that Mexicans view existence in a manner that "life is not to be enjoyed; it is to be endured. The Mexican expects life to be hard and demanding."

A theoretical perspective that we argue can help us understand how differential mortality and culture in Latin America interacted with each other is niche construction theory (Odling-Smee et al., 2003). Niche construction is the process by which individuals and populations modify their own and each other's niches through their activities. Many niches are stable and last, especially in populations with a largely stable culture, few technological changes, and little invasion or interpopulation interaction. Other niches, however, are largely unstable (Rowley-Conwy & Layton, 2011). Latin American niches for native populations, European settlers, and African populations brought as slaves were hardly stable, especially in the first century of contact because of frequent and intense changes in the genetic pool associated with microbial cross contamination.

Most noteworthy, however, is that patterns of niche construction in Latin America hardly follow textbook

classifications: it is impossible to classify them as either solely perturbational or solely relocational (terms introduced by Odling-Smee et al. [2003] to refer to modifications of a culture's surroundings and exposure to new environments, respectively). It is likewise impossible to classify them as either solely inceptive or solely counteractive to changes in the environment. This is because most models of niche construction describe how a population changes its niche, whereas the history of Latin America contains an intense interaction among populations and the generation of admixed individuals who introduced further diversity into the cultural and genetic pools. Changes introduced by one population into the environment include changes to other populations encountered and, through feedback, to their own constitution. Therefore, this can be characterized as a multidirectional set of changes.

Following the model of Rendell et al. (2011) for propagational niche construction of complexes of cultural practice and diseases, it can be argued that as initial contact between European conquistadors and Amerindians brought about the transmission of contagious diseases, microbial contamination risk led to increased migration as an avoidance strategy for microbial contamination, while migration spread diseases further geographically and thus reinforced more widespread contact among populations. In contexts in which a culturally transmitted response to contain disease propagation is not feasible, perhaps because the population lacks the requisite means for immediate cultural solutions, then a genetic response may occur (Laland & O'Brien, 2011), such as the admixture described here. Though migration as a result of increased microbial contamination might at first be considered simply a by-product rather than a constitutional aspect of the populations in this case, by-products can play an important evolutionary role by modifying selection pressures (though there is debate as to whether this should be considered niche construction formally or simply niche changing; see Dawkins, 2004).

Social and political forms of organization are also important aspects of a culture's niche and products of niche construction, too (Yamagishi & Hashimoto, 2016). In this sense, the social hierarchies and embedded (at least initially) interethnic slave relations in Latin America were an integral part of production and development in Latin American cultures and fostered the niche conditions for continued interbreeding. As such, they functioned as an aspect of the social configuration of Latin America that brought populations into

maintained and continuous contact in spite of, and perhaps facilitating, microbial contamination risk and thus the adaptive advantage of admixed individuals

In cognizance of the foregoing, this article presents how historical and cultural patterns present in colonial-era Latin America have impacted the genetics and culture of modern-day Latin America and the Caribbean. The history of Latin America is broadly summarized and then linked to genetic patterns of admixture based on the current literature. Additionally, we provide evolutionary mechanisms that may have shaped the pattern of gene flow in Latin America.

We first introduce the cast of characters, or dramatis personae. What were the three major biocultural groups that fused to form Latin America? We introduce the three ancestral populations of Europeans, Amerindians, and Africans. We then describe how the initial contact took place, leading to the conquest by the first group of the latter two. We then consider the sexual asymmetries involved in their hybridizations and relate them to the sociocultural circumstances of the exchange of genetic material. Finally, we describe the resulting patterns of genetic admixture and include a discussion of the nature of adaptive introgressions from one ancestral population to another, leading to the increase adaptive competence of the hybrids.

The next major portion of this article deals with the sociocultural conditions that defined the prevalent selective pressures during the period of gene-culture coevolution following the creation of the hybrid populations. First, we consider socioeconomic stratification among ethnic groupings consequent to the European invaders placing themselves at the top of the social hierarchy, as one might expect they would. Second, we consider the implications of this social stratification for the nature of the interethnic admixture that followed. Third, we consider the role of certain universals in human mating behavior, such as the principles of polygyny, hypergamy, and positive assortment by genetic similarity. Fourth, we consider the implications of interethnic admixture for health, which we believe were among the main drivers of selection among alternative hybrids.

Dramatis personae: The ancestral populations

At the time of Christopher Columbus's arrival in Latin America, Salzano and Bortolini (2002) estimated, there were approximately 43 million *Amerindians* inhabiting Mesoamerica and South America, with approximately 14 million in central Mexico and

13 million in the central Andes. The indigenous population in Latin America currently comprises about 58 million people, representing 10% of the total population of the continent, even when considering the likelihood of significant underreporting of these numbers. The indigenous population is divided among about 400 different linguistic groups.

The modern nation-states with the highest proportions of indigenous population are Mexico, Bolivia, and Guatemala. In Mexico, the proportion of indigenous language speakers has remained at around 10% of the national population. In Bolivia, about 62% of the population consider themselves *indígenas*. In Guatemala, the indigenous population is between 41% and 43% of the population (Hopenhayn et al., 2006; UNICEF, 2009). Nevertheless, major points regarding the indigenous peoples of the Americas must be made. The Americas, much like their people, are diverse and encompass a range ecosystems and climates (Kirkwood, 2000). This has many implications for culture and means of subsistence (Chasteen, 2004) and for adaptations to local ecologies and their immediate challenges. While much diversity in customs, appearances, and lifestyles exists among the indigenous groups of the Americas, we collapse these groups together to simplify the dynamic and multifaceted history of genetic and cultural upheavals in the Americas.

The arrival of *European explorers* to the Americas at the end of the fifteenth century served as a catalyst for the diffusion of European cultural ideals and technological innovations to the Amerindians. Aside from the introduction of culture, European explorers introduced diseases and genetic variability that was not present in the "New World," and they contracted native diseases that were not present in the "Old World" (Cochran & Harpending, 2010). As with the native Amerindians, the Spanish explorers and colonists were themselves diverse in their social classes and geographic regions of origin. Furthermore, while aristocratic families arrived in the New World during Spanish exploration, the majority of the passengers on Spanish expeditions were young males seeking status. For instance, Duncan's (1997) biography of Hernando de Soto described the "typical" profile of a Spanish explorer growing up in the province of Extremadura:

Extremadura produced such tough, no-nonsense men and women four and a half centuries ago, who not only survived when they traveled to America,

but thrived amidst the hardships of the conquista. Even today, extremeños area hardscrabble people—small, wiry, practical, and tenacious, representing the same extremes of Spanish poverty and vitality they did in Soto's era. (Duncan, 1997, p. 8)

It thus appears that the harsh, unpredictable environment of Extremadura produced individuals adapted to the rigors and danger of the vast, rugged terrain of the unknown Americas—consistent with evolutionary reasoning (Ellis et al., 2009). Duncan (1997) described the majority of Spanish explorers and colonists in central Mexico as originally hailing from the province of Extremadura. In contrast, the majority of early settlers in northern Mexico emigrated from the Spanish province of Andalucía, possibly because of the similarities in climate and ecology. This is evidenced by the fact that the flour tortillas commonly prepared in northern Mexico are derived from an imported Andalusian flatbread with its ultimate origins in the Levant (Nabhan, 2012), as opposed to the maize tortillas commonly prepared in central and southern Mexico that are of Amerindian origin. In the nineteenth century, an entirely new wave of immigrants came out of the northern Spanish provinces of Galicia and Asturias, to be followed later by another wave from the Basque Country. Only some of these later migrants went to Mexico, with large numbers of them settling in other former Spanish colonies such as Cuba (Family Tree DNA, 2016) and Argentina (Núñez Seixas, 2001).

Though it is known that the Norse landed in the Americas 500 years prior to the Spanish, the influence and impact of the "discovery" by the Spanish had long-term cultural, social, and genetic ramifications that are still present in modern-day Latin America (Chasteen, 2004; Ebenesersdóttir et al. 2011; Salzano & Bortolini, 2002). For instance, a recent paper provided evidence of the presence of Amerindian mitochondrial DNA (mtDNA) within a family line in Iceland. It appears that at least one of the early Norse travelers to North America brought a wife back to Iceland (Ebenesersdóttir et al., 2011).

The introduction of slave labor from parts of *Africa*, such as Guinea in West Africa, Angola in southwest Africa, and Mozambique in southeast Africa (Salas et al., 2004), further demarcated social hierarchies by race and ethnicity (Quijano, 2000) by placing African slaves in farming and other difficult tasks. The majority of African slaves were shipped to Brazil, to serve the Portuguese colonies. The second-largest group of slaves was shipped to Spanish colonies. Latin America, like colonial areas in

the United States, relied on the slave trade to provide workers who would extract products for the colonies and for their motherlands in Europe (Quijano, 2000). Further, the establishment, maintenance, and nourishment of colonial settlements in Latin America were time-consuming and arduous tasks that required large numbers of workers. Initially, indigenous populations were put to work constructing settlements and providing assistance in day-to-day activities. However, after the Spanish outlawed indigenous slavery (Wade, 2017b), European colonists began to import slaves to the Americas.

Contact and conquest

European conquest of what became Latin America upset the sociocultural systems and norms of the various tribes, nations, and empires in Mesoamerica and South America. At the height of the European expansion, fueled by imperial aspirations and Christian ideals, the invaders sought to subjugate and dominate the indigenous cultures of the Americas by destroying their religion and culture and exploiting their resources for market sale. For instance, a year after Columbus landed, a policy of indigenous slavery was implemented within the settlement (Churchill, 1997; Salzano & Bortolini, 2002), which led to a virtual (though unintended) genocide of the so-called Taino (Arawak) people by means of a combination of overwork and disease (de las Casas, 1552/2007).

Europeans were able to subjugate and convert Amerindians to Christianity, causing a shift in the culture, politics, and social structure of the Americas. The conversion of indigenous tribes to Christianity was another aspect of invasion and another European mark in the Americas for the Europeans; according to some scholars, "Christianity was a weapon of conquest, not a path to salvation" (Calloway, 1997, p. 70). Desperate for social cohesion and dwindling in numbers, the Amerindians converted to the "dominant" religion of the Europeans; however, while learning the word of Jesus, the Amerindians were subjected to beatings, forced to work, and sexually abused instead of experiencing goodwill (Calloway, 1997; Gutiérrez, 1985; Skidmore & Smith, 2005). The work that the natives did included raising and tending crops and building missions (Calloway, 1997).

The turn of events in Latin America produced a climate in which sexual exploitation of indigenous tribes was facilitated for European colonists. Wars and diseases affected the peoples of Latin America through the loss of large numbers of their members, but the losses were sex biased. The catastrophes of the Americas caused a large loss of males of reproductive age (Skidmore & Smith, 2005; Telles & Sue, 2009). To illustrate, a 1749 census of colonial Massachusetts of an indigenous tribe, while outside Latin America, showed that 20% of indigenous women were widowed, diminishing the male protection typically obtained from close kin and familial allies (Calloway, 1997). Migration to the Americas was sex biased as well (Chasteen, 2004; Skidmore & Smith, 2005). In Peru, European men outnumbered European women seven to one (Skidmore & Smith, 2005). Without the aid of related males, outside intruders, such as Europeans in Latin America, sought to control females and integrate them into the predominant patriarchal social structure (Skidmore & Smith, 2005; Smuts, 2007). Such male vigilance in protecting female kin, in later years, translated into the *machismo* that is common in modern-day Latin American culture (Ingoldsby, 1991; Skidmore & Smith, 2005). In the Southeast, Spanish conquistadors were known to abduct native women, and intercourse among European males and native females was common. Additionally, priests and friars, who were supposed to remain chaste and convert the natives, sometimes had children with native women (Calloway, 1997; Skidmore & Smith, 2005). This pattern is in stark contrast with the case of the *filles du roi* in Canada, who were young women shipped to the colony by the French king as wives for the male colonists, diminishing the need to marry local women (Gagné, 2000).

The loss of native populations resulted in a decline in colonial economic labor, which was the driving force behind the colonies' development and stability. During and almost immediately after the loss, Spanish colonialists began to ship African slaves to the Americas—mostly to Central and South America and the Caribbean (Skidmore & Smith, 2005; Smith, 1997). By the sixteenth century, African slaves were used to manage the lucrative Portuguese sugar crops that were being planted in South America and the Caribbean (Skidmore & Smith, 2005). By 1825, Blacks made up 11.9% of the population in the Spanish colonies and 49.8% in the Portuguese colonies, as a result of the importation of African slaves and subsequent childbirths (Skidmore & Smith, 2005).

Genetic admixture of populations

The previous sections summarized the historical upheavals of Latin America, where the "discovery" of the New World by European settlers created social upheavals for Amerindians present in Mesoamerica and

South America in the late fifteenth century. Additionally, we summarized the selection pressures that may have shaped the mating systems in early Latin America. This section links the history of the Americas to mating configurations by providing genetic evidence for the scenario that we described (for an in-depth review of admixture and gene migration in Latin America, see Sans 2000).

Before the arrival of the Iberians in the late fifteenth century, it is possible that Amerindian tribes in the Americas mated and traded culture with each other. Though most tribes practiced endogamy among their members, there is evidence of mating occurring between Amerindian tribes (González-Martín et al., 2008). However, the arrival of European explorers, a distinct population in the New World, resulted in social and mating system shifts that are reflected in genetic evidence. Genome-wide analyses of current Latin American populations indicate that multiple periods of gene flow have shaped the pattern of admixture that we are about to describe, with sizeable pulses of European migration and introduction of African ancestry over a wide time range, from approximately 3 to 14 generations ago (Homburger et al., 2015; Kidd et al., 2012).

Sex-biased hybridization

In evolutionary/population genetics, when two distinct populations separated by space, geography, and culture mix, the phenomenon is known as *genetic admixture*, which is "the formation of a hybrid population through the mixing of two ancestral populations"; thus, Latin America can be viewed as a society made up of "hybridized," mixed-ancestry individuals (Chakraborty, 1986; Jobling et al., 2013, p. 609). In the case of Latin America, we witness a preponderance of one specific type of genetic admixture—sex-biased admixture—whereby ancestral populations contribute differently based on their sex (Jobling et al., 2013). When detecting sex-biased admixture in the population, researchers seek the following patterns of inheritance in loci of the genome:

If females contributed more than females to an admixed population, estimates of admixture would like on a gradient: mitochondrial DNA > X chromosomes > autosomes > Y chromosome.

By contrast, if males contributed a greater proportion, the gradient would be reversed: Y chromosome > autosomes > X chromosomes > mitochondrial DNA. (Jobling et al., 2013, p. 465)

European males in the Americas controlled more resources and had more social power than the dwindling Amerindian males, as previously noted. For Latin America, we would expect to see a high prevalence of European alleles that are paternally derived versus indigenous (and, in the case of the Caribbean and South America, African) alleles that are maternally derived. When the genetics of Latin America are tested, the results confirm the observed patterns based on history (Adhikari et al., 2016; Adhikari et al., 2017). For instance, early studies in which ABO Rh(D) blood groups were tested, such as in Monterrey, Mexico, the research supported the basic assumption that individuals in Latin America were mixed with European and indigenous blood (Garza-Chapa, 1983). The limitation of blood group experiments is that researchers could not determine *who* (male or female) contributed to the admixture of the population.

In later years, the research became more refined and the genetics methodology more sophisticated. Most research on genetic admixture in Latin America (and around the world) so far has focused on microsatellite genome data or X chromosome data (Wang et al., 2008), mtDNA (Green et al., 2000), and Y chromosome data (Leite et al., 2008). Recent studies have examined genome-wide patterns on single nucleotide polymorphism and haplotype in individuals across Latin American countries, also confirming the sex bias in historical hybridization (Bryc et al., 2010). Mitochondrial DNA can be inherited only from the mother, and the Y chromosome can be inherited only from the father. Thus, by comparing the origins of the DNA in the Y chromosomes and the mitochondria, it is possible to directly determine the male and female populations of origin. The X chromosome is a special case in that it is a less sensitive indicator of male versus female ancestry, as one-third of the X chromosomes in a generation would be expected to have come from the fathers and two-thirds of them from the mothers.

The story that we reconstruct from these analyses is surprisingly similar for the great majority of Latin American populations studied: the patrilineage, broadly, has been primarily of European descent, while the matrilineage has been of indigenous or African descent, such as in Argentina (Martinez Marignac et al., 2004), in most of Brazil (Bortolini et al., 1999; Leite et al., 2008), in Chile (Rocco et al., 2002), in Colombia (Bedoya et al., 2006; Rojas et al., 2010), in Costa Rica (Carvajal-Carmona et al., 2003), in Mexico (Lisker et al., 1995), and in Uruguay (Sans et al., 2002). For example, Morera

et al. (2003) tested the polymorphisms of 32 alleles or haplotypes of 11genetic systems, including the blood groups ABO, Rhesus (Rh) in 2,196 individuals originating from five distinct regions of Costa Rica. They found that the relative proportions of genes in the population of Costa Rica as a whole indicated 61% European, 30% Amerindian, and 9% African ancestry.

Exceptions exist, such as some rural populations studied in Venezuela, where Amerindians have been found to have contributed exclusively through males, whereas females tended to be of African descent, and parts of the population in the extreme south of Brazil, in which the maternal and paternal sides indicate almost complete European ancestry (Bortolini et al., 1999). A rough estimate indicated that Black Latin Americans and Afro-mestizos (three-way admixtures of European, African, and Native American) represent about the 30% of the total population, or about 174 million people (Antón et al., 2009), most of them living in Brazil (50%), Colombia (20%), and Venezuela (10%).

The majority of the genetic studies in most populations, however, support the predictions of sex-biased ethnic contributions (see Adhikari et al., 2016; Adhikari et al., 2017), as do historical archives of the marital unions happening throughout the regions of colonial Latin America (e.g., de Saint-Hilaire, 1961; Isola, 1975). Additionally, in many regions, such as the Río de la Plata region (including Uruguay, part of Argentina, and southern Brazil), it is known that slaves were needed for work thought to require women more than men, which prompted large numbers of Black women to be imported (Isola, 1975). This corroborates the expectation of sex-biased genetic contributions to modern local populations.

In brief, based on the current literature on genetics in Latin America, we can come to two general conclusions. First, the genetic composition of Latin America is *not* homogenized and is, instead, a unique genetic mixture of the past distinct cultures that inhabited Latin America—mainly, European explorers, Amerindians, and African slaves. Second, the genetic admixture was sex biased. Based on the research that we have reviewed, we can conclude that, broadly, in Latin America, patrilineally derived genes were of European ancestry, while matrilineally derived genes were mostly of Amerindian descent.

Molecular genetic evidence for Dutton's rule

An enigmatic figure in Mexican history, *La Malinche* has been both praised for her work in saving the lives of many indigenous people and vilified for her assistance in Hernán Cortés's conquest of the Mexica civilization ruled by the Aztec Confederation (McBride-Limaye, 1988). Whether one considers her a heroine or a traitor to her people, one must acknowledge that she symbolizes the sociocultural and genetic upheavals experienced by Mexico and much of Latin America and the Caribbean. Malintzin, her proper name in Nahuatl, bore a son to Cortés and became the ceremonial "Eve" of *mestizaje*, reflecting the identity, culture, and history of modern-day Latin America and the Caribbean and the people there (Candelaria, 1980; McBride-Limaye, 1988). La Malinche's story reflects a common mating pattern present in colonial-era Mexico and the rest of Latin America. Indigenous young women gave birth to children of Spanish explorers, usually out of wedlock (Skidmore & Smith, 2005), creating a hybridized culture and people known as *hijos de la chingada*, to emphasize their extramarital origins (Sanchez, 1998; Smith, 1997).

The situation in Latin America is by no means unique. In an archival study of cross-national marriages involving Finnish men and women, Dutton and Madison (2017) found a systematic tendency for Finnish men to disproportionately marry women from lower-status nationalities and for Finnish women to disproportionately marry men from higher-status nationalities, as indicated by measures of human and economic development. For example, more Finnish men marry Thai women than Finnish women marry Thai men, whereas more Finnish women marry British men than Finnish men marry British women. Dutton and Madison interpreted this asymmetrical pattern as generated by the phenomenon of female hypergamy (see Bokek-Cohen et al., 2008; Cashdan, 1996; Hatfield & Sprecher, 1995; Saint-Paul, 2015), as applied to cross-national differences in socioeconomic status.

This finding motivated us to examine the generality of *Dutton's rule* across historical human societies, wherein cross-ethnic hybridizations are asymmetrically sex biased, disproportionately occurring between men from higher-status groups and women from lower-status groups (Edward Dutton, personal communication, London, May 12, 2017). The historical examples of this principle that we found were rarely based on the sophisticated quantitative measures of socioeconomic status used by modern industrial societies, but were instead based on which ethnic group was migrating, invading, conquering, displacing, or otherwise expanding at the expense of the other. We relied primarily on molecular genetic evidence comparing Y-chromosomal haplogroup

data (exclusively indicating the paternal lineage) with mtDNA haplogroup data (exclusively indicating the maternal lineage) for each hybridized population of interest.

Using this approach, we found the molecular genetic footprints of 10 well-known historical examples of such cross-ethnic hybridizations, each of which was fully consistent, without exception, with Dutton's rule:

1. The molecular genetic footprints of African slavery in both North America and Southwest Asia (the Arab Mashriq), indicated by a preponderance of European Y-chromosomal haplogroups coupled with a preponderance of sub-Saharan African mtDNA haplogroups in modern African American populations (Lind et al., 2007) and by a preponderance of Southwest Asian (Mashriqi Arab) Y-chromosomal haplogroups coupled with a substantial proportion of sub-Saharan African mtDNA haplogroups in modern Mashriqi Arab populations (Richards et al., 2003);

2. The molecular genetic footprint of the Neolithic Bantu expansion from West Africa, indicated by a preponderance of West African Y-chromosomal haplogroups coupled with a preponderance of aboriginal mtDNA haplogroups in sub-Saharan Africa (Berniell-Lee et al., 2009; Gignoux et al. 2011; Li et al., 2014; Rowold et al., 2014; Wood et al., 2005);

3. The molecular genetic footprint of the Islamic imperial Arab expansion into the North African Maghreb, indicated by a preponderance of Arabian Peninsula Y-chromosomal haplogroups coupled with a preponderance of aboriginal mtDNA haplogroups in the North African Maghreb (Chiaroni et al., 2010; Regueiro et al., 2015; Triki-Fendri & Rebai, 2014);

4. The molecular genetic footprint of the Southwest Asian Neolithic expansion into Europe, indicated by a preponderance of Southwest Asian Y-chromosomal haplogroups coupled with a preponderance of aboriginal (Paleolithic European) mtDNA haplogroups in Europe (Balaresque et al., 2010; Chikhi et al., 2002; Fernández et al., 2014; Francalacci et al., 2010; Lacan et al., 2011; Richards et al., 2000; Semino et al., 2000; Sjödin & François, 2011; Torroni et al., 2001);

5. The molecular genetic footprint of the Anglo-Saxon invasion and migration into Britain, indicated by a preponderance of Anglo-Saxon Y-chromosomal haplogroups coupled with a preponderance of aboriginal (native British) mtDNA haplogroups in Britain (Weale et al., 2002);

6. The molecular genetic footprint of the Ashkenazi and Sephardic migration into Europe, indicated by a preponderance of Southwest Asian (Levantine) Y-chromosomal haplogroups coupled with a preponderance of aboriginal (Paleolithic European) mtDNA haplogroups in European Ashkenazi and Sephardic Jews (Costa et al., 2013; Nebel et al., 2001);

7. The molecular genetic footprint of the Indo-European expansion from Central Asia into the Indian subcontinent, indicated by a preponderance of Central Asian–derived Ancestral North Indian (ANI or Aryan) Y-chromosomal haplogroups coupled with a preponderance of aboriginal Ancestral South Indian (ASI or Dravidian) mtDNA haplogroups in Indian subcontinent (Basu et al., 2016; Reich et al., 2009; Silva et al., 2017; Zhao et al., 2009);

8. The molecular genetic footprint of the Indo-European expansion from Central Asia into Iran, indicated by a preponderance of Central Asian–derived Indo-European (Aryan) Y-chromosomal haplogroups coupled with a preponderance of aboriginal Southwest Asian (Arabian Peninsula–derived) mtDNA haplogroups in Iran (Terreros et al., 2011);

9. The molecular genetic footprint of the Northern Han expansion into southern China, indicated by a preponderance of Northern Han Y-chromosomal haplogroups coupled with a preponderance of aboriginal mtDNA haplogroups in southern China (Nothnagel et al., 2017; Wen et al., 2004; Xu et al., 2009); and

10. The molecular genetic footprint of the Mongolian imperial expansion into Central Asia, indicated by a preponderance of Mongolian-derived Y-chromosomal haplogroups coupled with a preponderance of diverse aboriginal mtDNA haplogroups in Central Asia (Brissenden et al., 2015; Dulik et al., 2011; Katoh et al., 2005; Zerjal et al., 2002; Zerjal et al., 2003).

In many of these cases, the sexually asymmetrical pattern of admixture produced by the action of Dutton's rule left a cline that is detectable to this day. For example, one may still observe clines in India of decreasing preponderance of ANI in proportion to ASI genes going (1) from north to south and (2) from upper to lower caste (Reich et al., 2009).

Socioeconomic stratification among racial and ethnic groupings

A general consensus exists among sociologists and historians that current conceptualizations of social stratification based on skin color and phenotypic characteristics have their roots in the sixteenth to eighteenth centuries. The discovery, conquest, and colonization of the Americas by European nations contributed to the ideology of ethnic superiority among conquistadors (Wade, 2008). While the conquest was characterized by the subjugation and extermination of the cultures of indigenous peoples, the stratification of society was associated during the colonial process with the ideology of superiority of the European groups (Chasteen, 2004). Based on this, a social pyramid was built in which the lowest rung was occupied by African slaves and the top rung was occupied by the *lusohispanos*, which includes lineages originally derived from either Portugal (formerly Roman *Lusitania*) or Spain (formerly Roman *Hispania*). Indians and mestizos were halfway between these two (Wade, 2008).

Later, the nation-states that were established in the nineteenth century tried to overcome the hierarchical structures of the colony under the flag of a single culture and a single nation, which also served to promote national homogenization. However, the building of national identity degraded the integrity of the indigenous and African cultures through forced assimilation or even extermination by the new Latin American elites (Soto Quirós, 2009). On the other hand, ideologies pertaining to the inferiority of these groups consolidated during this period. Thus, according to some authors, the key to understanding racial interactions in Latin America is that racism and racial admixture coexist and interweave (Wade, 2008; for a discussion of racism, *mestizaje*, and national identity, see Moreno Figueroa, 2010,).

Thus, long-term structural discrimination has important implications for the contemporary situation of indigenous peoples and African-descendant peoples in Latin America. Despite the significant improvement of their situation in the last few decades, indigenous peoples and minorities (such as African-descendant communities) continue to experience disproportionate levels of poverty and marginalization and have limited access to basic resources such as work, education, and health care.

Overall, the incidence of extreme poverty among indigenous peoples and African-descendant groups exceeds the rate of the rest of the population, excluding the cases of Costa Rica and Haiti, where ethnicity does not seem to imply profound differences in levels of poverty. In Brazil, for example, the proportion of African descendants living below the poverty line is twice as high as the proportion of non-African-descendant people living in the same condition (Antón et al., 2009). Indigenous peoples and Afro-Latin and Afro-Caribbean populations score the worst on economic and social indicators and, to a large extent, are the poorest in the region (Del Popolo et al., 2011). In Mexico, for example, more than 50% of the households in indigenous regions have no electricity, 68% have no running water, and 76% have no floors. In Honduras, illiteracy among indigenous groups reaches 87% (Hopenhayn et al., 2006).

It must be said that in the English-speaking Caribbean (Belize, Dominica, Guyana, Saint Lucia, Saint Vincent and the Grenadines, and Trinidad and Tobago), the social situation of Afro-descendants is different from that found in the rest of the region. They do not experience the strong exclusion of the continental Latin American societies, thanks to the fact that they represent the demographic majority, as a result of structural changes during the independence period and, particularly, because of equality in access to education. Nevertheless, according to some estimates of poverty, in Caribbean countries such as Guyana and (to a lesser extent) Dominican Republic, ethnic disparities also exist (Hopenhayn et al., 2006).

A key aspect of the poverty experienced by indigenous and Afro-Latin households is the precarious employment rate of these groups. Specifically, the main problems faced by indigenous peoples and Afro-Latins are unemployment, low-quality jobs, and systematic pay gaps in relation to nonindigenous people. In Brazil, for example, unemployment is around 5% of the economically active population; the percentages for women and Blacks are always much higher than those for men and Whites, respectively. In Bolivia, about 65% of precarious jobs and 25% of semiskilled jobs are occupied by *indígenas*. Similarly, only 4% of indigenous people occupy jobs that require higher qualifications (CEPAL, 2014).

Access to formal education is commonly used as a proxy for discrimination and social exclusion in Latin American demographic and sociological analyses. Disparities in access to education are another element characterizing the Latin American context. Overall, the average schooling of indigenous and Afro-Latins is lower than that of nonindigenous or African descendants in Latin America. In Guatemala, the average schooling of the indigenous peoples is more than two years less than the average schooling for the rest of Guatemalans

(Adams, 2005). In Brazil, the rate of functional illiteracy among Afro-Brazilians (men and women) is higher than that of Whites of both sexes (12% and 7.2% compared with 5% and 3.5%, respectively). Among indigenous people, the relative incidence of functional illiteracy is somewhat higher for both men and women (16.5% and 11% respectively; see Antón et al., 2009).

Regarding health, data reveal that indigenous peoples in Latin America have a much deteriorated health condition compared with the rest of the population. Indigenous households, particularly those living in rural areas, often face high risk of disease because of poor living conditions and limited availability of health services, water and sanitation (CEPAL, 2014).

For example, indigenous infant mortality remains consistently higher than among the nonindigenous, and indigenous peoples are far from achieving equality in the entire region, with the exception of Costa Rica. The greatest inequalities are present in Panama and Peru, where the indigenous infant mortality rate is three times the nonindigenous rate, and in the plurinational state of Bolivia, where it is more than double. Specifically, Costa Rica and Uruguay report the lowest mortality rate among indigenous children, with 11.5 and 15.8 per 1,000 live births, respectively. At the other end lie Panama and Guatemala, with 46.4 and 55 per 1,000 live births, respectively; the most dramatic situation is Bolivia, where 77 indigenous children in 1,000 die before the age of five (CEPAL, 2014; OPS, 2012).

On top of these structural socioeconomic differences *between* these ethnic classifications, there is also the question of discrimination even *within* these broadly defined groupings. Ideologically, for example, Mexico has no racial hierarchies and avoids defining individuals based on phenotypic variation. Nonetheless, Mexico unofficially has a social stratification organization based on skin color and phenotypic differences (Villarreal, 2010), as do many other modern nation-states in Latin America and the Caribbean (Lynn, 2008; Telles, 2014). Recent research suggests that darker-skinned individuals in Latin America have lower educational attainment, even while controlling for sociodemographic factors (Telles et al., 2015). This pattern has also been found among Asians and Latinos residing in the United States (Ryabov, 2016).

In general, social stratification, prejudice, and discrimination have been empirically linked not only to limited access to housing, education, and employment but also to stress, diminished physical and mental health, reduced personal satisfaction, and low self-esteem

(Smith-Castro, 2010). Nevertheless, data also suggest that under certain conditions, ethnic minorities cope with the negative consequences of stratification and discrimination by increasing identification with the in-group and that a strong sense of ethnicity has protective features (Smith-Castro, 2005).

In addition to social factors, this pattern of educational attainment has an impact on health. Researchers have extensively documented a phenomenon dubbed *the SES-health gradient* across areas around the world, including (but not limited to) the United States and the United Kingdom (Adler & Stewart, 2010; Marmot et al., 1991; Williams et al, 2010). Individuals with lower socioeconomic status (SES), most notably racial and ethnic minorities, succumb to illness and chronic health issues sooner than Whites and individuals with higher SES. Many structural and behavioral mechanisms have been proposed for this association such as access to high-quality health care, better access to high-quality food, lower exposure to stressors, and increased health-maintaining behaviors (e.g., not smoking, exercising, consuming fruits and vegetables; see Bird et al., 2016).

Research across Latin American countries attempting to document this health gradient has been inconsistent. For instance, research investigating substance use in Mexican adolescents found that higher levels of subjective community social status (one's status relative to one's community) were associated with *increased* smoking and drinking; conversely, higher levels of subjective societal social status (one's status relative to Mexico) were associated with decreased smoking and drinking (Ritterman et al., 2009). A similar pattern was found in relation to socioeconomic status and blood pressure in low-income Mexican women. Paradoxically, higher household income was weakly but positively associated with higher systolic blood pressure ($r = .04$). On the other hand, educational attainment was negatively associated with systolic blood pressure ($r = -.13$; Fernald & Adler, 2008). As these authors have suggested, these markers of SES may connote different structural and behavioral mechanisms in a *developing* country as opposed to a *developed* country.

Further inconsistencies exist when examining health disparities within Latin American countries. Mexican citizens with indigenous ancestry have lower odds for obesity and diabetes than nonindigenous Mexicans (Florez et al., 2009). Further, communities with high proportions of indigenes have lower odds of obesity and diabetes (Stoddard et al., 2011). This is in stark contrast with the situation in the United States, where

indigenes (Native Americans) have higher odds of obesity and diabetes (e.g., Burrows et al., 2000; Vijayakumar et al., 2018). Further, medical research has indicated that in the United States, more indigenous admixture produces higher risk for obesity and diabetes, suggesting that there may be a phenotypic or an environmental mismatch between indigenous genes and the dietary environment in more developed countries (e.g., the "supermarket diet" rich in processed foods, fats, and sugars; Santiago-Torres et al., 2017). Nevertheless, a large-scale analysis that examined skin tone and self-reported health status in Brazil, Colombia, Mexico, and Peru showed a significant gradient in self-rated health by skin color (those with darker skin colors reported poorer health); it also showed that the darker skin color effect on self-rated health was mediated by increasing exposure to class discrimination and low SES (Perreira & Telles, 2014).

These discrepant results collectively indicate that inter-ethnic admixture in Latin America may have costs as well as benefits that are conditional on the social context.

Implications of stratification for admixture

Based on what we know from past research and its synthesis in the present article, specific hypotheses relevant to genetic admixture can be generated, particularly focusing on the impact of sex-biased admixture and sexual selection/assortative mating in Latin America. One major issue regarding the inquiry into mating in Latin America is that ethnicity and ancestry are unfortunately also associated with social strata and the dynamics present within Latin American culture (Salzano, 2004). Indeed, much research has documented a link within Latin America between ancestry, indexed by genetic markers, and social class, with individuals possessing a higher proportion of indigenous and/or African ancestry most likely to reside among the lower social strata (Garza-Chapa, 1983; Lisker et al., 1995). While there is evidence of ethnic endogamy, the confound between ethnicity and social strata makes it likely that individuals could be selecting mates based more on social class and less on ethnic similarity. Although it is very difficult, future research should design genetically and socially informed studies that allow for the deconstruction of ancestry and social class to examine whether the magnitude of endogamous mating in Latin America is greater for social class or genetics. Risch and colleagues (2009) argued that the present ecology places constraints on mate selection and preferences, such that humans can only select mates who reside in close proximity, which typically ends up being people who *look*, *act*, *think*, *and live like oneself* (i.e., similar ethnicity and social class).

Men have been shown to have a greater preference for lighter skin in women and women a preference for darker skin in men (Aoki, 2002; Feinman & Gill, 1978; Jha & Adelman, 2009). Theoreticians have argued that this skin preference pattern may be a product of sexual selection (Aoki, 2002; Feinman & Gill, 1978). Should it be the case that skin tone preferences are sexually selected, it is then possible that these preferences, over time, shape the genetic and ancestral makeup within and between social strata. As some evolutionists have argued, social ranking, in highly class-stratified societies, may produce more pronounced pigment gradients, resulting in a "lighter" higher class and a darker lower class (Symons, 1995). The reason behind the change is that women with lighter skin, who usually have higher levels of European ancestry, have a greater chance of hypergamy, or marrying "up" socially—causing a change in genetic patterns across generations and, possibly, diverging genetic proportions in social classes—and that darker-skinned women continue to marry within their class of origin.

It is important to note another mode of admixture: not all European settlers were elite or of high social standing. It was these settlers who often integrated into and adopted the culture of the indigenous and African individuals residing in the lower stratum, mated, and produced admixed children (Chasteen, 2004, p. 82). Though past research (Frisancho et al., 1981) has found no link between skin color and X chromosome heredity, future research may want to continue to investigate whether parents of a specific sex contribute to the skin color of opposite-sex children.

Polygyny, hypergamy, and assortative mating

Polygyny is a mating arrangement in which one male has multiple female mates. Typically, such an arrangement, when viewed androcentrically, might seem to be beneficial only to males—as males will invest little in offspring and having multiple children (Orians, 1969; White & Burton, 1988). Though males do invest little in multiple children in polygynous arrangements, the mating structure is often fueled by female choice—in order for polygyny to become beneficial to males, females must confer benefits from such a mating orientation (Orians, 1969; White & Burton, 1988). Theoretically, for polygyny to be maintained within a population, certain selective pressures must be present in the

environment for women to voluntarily participate in such arrangements. For example, it is important to distinguish clearly between a form of polygyny in which male investment is minimal (e.g., the roaming conquistador who impregnates women in every village he conquers) and the harem system practiced in the Middle East, which involves stable marriages and requires stable male wealth and high investment in wives and children, as well as occasional guarding by eunuch slaves. In Muslim cultures, any child sired by a Muslim father, even if born to a non-Muslim concubine, must be raised as a Muslim and admitted full and equal entry into the community of Islam (Ali, 2012; Hourani, 2013).

For instance, in ecologies where there is a disproportionate dispersal of resources, usually among males, it is in the female's best interest to find a mate who has the most to share with his offspring. In *resource defense polygyny* (Emlen & Oring, 1977), which is common in many diverse animal taxa (Alcock, 2009) and argued to be common among human societies (Hartung, 1982), males seek to monopolize females and their sexuality by monopolizing resources, with a select amount of males closely guarding territories of abundant and high-quality resources that can assist females in reproduction and child-rearing—although males in resource defense polygyny typically do not *directly* assist in child-rearing. Female choice, in environments where resource defense polygyny is present, must then attune to cues of quality defense of resources and quality resources. Selecting males who have the most resources would be the most advantageous choice for females (Buss, 1989; Emlen & Oring, 1977); however, in environments where a select amount of males monopolize the resources, mated males may only be the viable, advantageous option (Orians, 1969). For women, getting a smaller proportion of resources from well-resourced mated males is better than "a little of nothing" from males who have no mates or no children, a possible by-product of having nothing to contribute to a viable mate. Of course, this means the existing mate must be tolerant of the new situation, presumably if he is under similar selective pressures and facing similar choices to the additional mate.

In polygynous environments, males who monopolize resources probably are also able to defend resources because of their higher social status, greater health and fitness, and, possibly, intelligence. As Emlen and Oring (1977), pointed out, female choice is contingent not only on men who have resources but on men who can *keep* resources. Resource defense polygyny is expected especially when there is extreme inequality in male socioeconomic status (Pribil & Searcy, 2001; Ptak &

Lachmann, 2003). The *polygyny threshold model*, for example, predicts that when male economic inequality reaches a certain point, women will prefer becoming one of the many wives of a rich man over becoming the only wife of a poor man (Orians, 1969).

Another selection pressure for polygyny is the operational sex ratio in the population (Kvarnemo & Ahsejö, 1996; Orians, 1969; White & Burton, 1988). The operational sex ratio is defined as "the ratio of males to females ready to mate." When there is a disproportionate amount of organisms of one sex, the intensity of competition for mates among members of the other sex increase (Kvarnemo & Ahsejö, 1996). For instance, female-biased sex ratios (i.e., areas with a greater proportion of females to males) would generate greater female intrasexual competition for access to mates. Kvarnemo and Ahsejö (1996) proposed a theoretical interpretation of what would happen with a disproportionate operational sex ratio: the intensity of competition would increase among females when there are more females than males ready to mate in the immediate vicinity.

The selection pressures mentioned for polygyny were present in the early history of Latin America. Specifically focusing on polygyny in humans, White and Burton (1988) noted that higher male mortality (often due to warfare), capturing of women, plunder, and appropriation of resources were often characteristic of polygyny in humans. These factors were clearly present in early Latin American history, based on the evidence presented. In colonial Latin America, a disproportional operational sex ratio was experienced. Because indigenous male populations declined as a result of disease, genocide, and warfare, indigenous females were left with fewer viable *indigenous* mates. Moreover, European males, though possibly fewer in number than indigenous and African-descendant females, were controlling high-quality environments of abundant resources, and this led indigenous females to mate with European males, even when they were presumed to be celibate, as in the case of some European priests (Pimentel, 2005).

Nevertheless, we propose that the pattern of extralegal functional polygyny that continues to be prevalent in Latin America, at least for high-status men, has been maintained long past the era when violent conquest and enslavement occurred mostly by hypergamous mating. This latter process can be considered at least partly voluntary, although it might be driven by economic need on the part of women. In addition, under the polygyny threshold model, this process is also driven by socioeconomic inequality between men.

Male polygynous mating and parenting strategies in social context. The dynamics of ethnicity and social privilege provided a complex interaction that resulted in unique social stratification rules. Among the elite were the European-born Spaniards, who often had tense relations with the American-born Spaniards within the colonies, battling for social status and prestige (Skidmore & Smith, 2005). Between ethnic groups, social stratification rules (e.g., the most prestigious group was the Europeans, followed by mestizo populations, followed by natives; see Gutiérrez, 1985; Telles & Sue, 2009) led to low occurrences of mixed-ethnicity marriages (Skidmore & Smith, 2005). If interethnic marriage occurred, Spaniards would typically marry mestizas but rarely natives. In most cases, no legal marriages occurred among ethnic groups, but many Spaniards, like Cortés, kept native or mestiza mistresses. The main pattern of ethnic admixture should therefore be more properly referred to as one of *interbreeding* rather than *intermarriage*. Among the Portuguese, the same rules applied but included mainly African slaves, as was the case in the Spanish Caribbean.

Thus, such social stratification rules had implications for sexual politics and admixture, which thus influenced and altered the very rules that had originally influenced them. The elites (i.e., Europeans) in the colonies would thus guard the honor and integrity of their elite women to preserve them for marriage; for lower-class women, such as African slaves and natives/mestizas, extramarital affairs, which included either immediate rape or extended concubinage, were common (Chasteen, 2004; Smith, 1997).

As social class and ethnic ancestry are linked in Latin America, it is possible that mistresses may actually have a *higher* proportion of indigenous/African genes than the actual wives. For instance, Stevens (1973) noted that in Puerto Rico, a "middle-class man can easily afford a mistress from the working class," where "poverty is so widespread that many individuals live on the border of starvation" (Stevens, 1973, p. 60). Women in a situation of poverty may benefit from a male buying "her a few clothes," with "many of them entertain[ing] the hope that they can somehow persuade the men to divorce their present wives and marry them" (Stevens, 1973, p. 60). Although most males in their *casa principal* (main home) will invest highly in their family, upper-class males with more resources (money) to expend are able to maintain *casas medias* and *casas chicas*, where they support mistresses and possibly illegitimate children (Chasteen, 2004). Thus, it is possible that genetic admixture in Latin America could have implications for parenting and investment across groups.

As time passed and admixed individuals became reproductive, the dynamics of mating and parenting would have changed. A stereotype that is prevalent within Latin America is that males are expected both to be virile and aggressive (e.g., *machismo*) and to be highly supportive of and invest in their family (e.g., *familismo*; Stevens, 1973). As described in Cabeza de Baca et al. (2014, p. 539),

> One component of traditional Latino culture (especially among Mexicans and Mexican Americans) that is purported to exist by scholars is the concept of machismo that emphasizes structured gender roles between men and women and a rigid power hierarchy where men dominate, at the family- and societal level (Cromwell & Ruiz, 1979). Despite this widespread belief, many scholars emphasize that the concept of machismo may be overemphasized (Cromwell & Ruiz, 1979; Torres, Solberg, & Carlstrom, 2002). Still other scholars argue that concept of machismo among Latino cultures may have become denigrated when utilized by mainstream researchers (Mirande, 2004) and the "positive" components of the term ignored (Mayo, 1997).

Though the ideals of *machismo* and *familismo* might seem contradictory, they typically occur simultaneously, as illustrated by the prevailing attitudes toward male extramarital affairs.

With a polygynous arrangement, men may, through class, be selecting extramarital partners with, as mentioned, a lower degree of European ancestry from the wife and from themselves; additionally, although Stevens (1973) mentioned that men rarely leave their wives for mistresses, it is possible that when men do, they are "moving up" to a mate with either a more similar ancestry or a higher proportion of European genes. Sex ratios may also be biased, following the Trivers-Willard hypothesis. In households with more investment, often the main upper-class house, there will be a higher proportion of males. In the *casas medias* and *casas chicas*, we will witness a higher amount of female illegitimate children. It is important to note, however, that research testing the Trivers-Willard hypothesis in humans has produced extremely mixed results. For instance, while there is evidence to suggest that well-resourced individuals such as billionaires (Cameron & Dalerum, 2009) or taller

parents (Kanazawa, 2005) conform to the predictions of the Trivers-Willard hypothesis, there are also varying degrees of support from other populations (e.g., Davis et al., 2007; Guggenheim et al., 2007; Keller et al., 2001).

Evidence in early Guadalajara, Mexico, points to these hypothesized extramarital patterns. In early Guadalajara, the rate of illegitimate children was 40%. When broken down by ethnicity, the majority of illegitimate children occurred in the mixed-ancestry population (two-thirds) and among African slaves (four-fifths) than in the Spanish caste (one-quarter). Additionally, more illegitimate children were born among the poor class than among the rich (Hecht, 2002). If such a mating pattern occurs in Latin America, it would make more sense for males to invest highly in male offspring, who have more reproductive variability and must garner more resources to gain mates compared with female offspring (Bateman, 1948). Accordingly, the rich and turbulent history of Latin America can clearly be reflected in the mating patterns of early inhabitants and modern-day Latin America.

Female hypergamous mating and parenting strategies in social context. After the European conquest, single women purportedly headed many households in the New World (Skidmore & Smith, 2005; Smith, 1997). It is possible that this trend was the result of extramarital births (in the case of indigenous and African households) and widowed wives (in the case of the European settlers) who lived off the inheritances of their deceased husbands. Smith (1997) contended that "patriarchal" nuclear families were more common among the higher class and less so among lower-class (typically, mestizo, native, or African) households. Based on the historical evidence and the selection pressures for polygyny present in Latin America, molecular genetics should be the perfect tool to further explore whether such hypotheses are correct. Whereas the proportion of single-parent households began to increase considerably among African Americans in the United States only after the mid-twentieth century, before which time most African Americans lived in reasonably stable families, single-parent households were not as much of a novel phenomenon in Latin America, where they have persisted since early colonial times. Nevertheless, recent increases in single-parent households have occurred in many parts of Latin America, such as Costa Rica (Rodríguez, 2008).

Furthermore, with native men dwindling and tribal numbers diminishing, indigenous females consciously sought to raise Native American numbers. Because of the new social structure introduced by Europeans, women, who had some influence in their communities, had to rely on males for status—with European males having the most status (Calloway, 1997). By mating with a European man, they would confer a social benefit to the offspring while culturally keeping the "ethnicity" of their mother. Within Portuguese settlements, intermarriage was rare. As in colonial New Spain, the Portuguese would take African-descendant, and to a lesser degree Amerindian-descendant, mistresses and produce extramarital children (Pimentel, 2005; Skidmore & Smith, 2005; Smith, 1997), in spite of the existence of prejudice and prohibitions on mating between Amerindian women and African-descendant men in some colonial Latin American regions (Bastide, 1974).

In addition to women's *active* choice of sexual partners, many indigenous and African women were enslaved, subjugated, and raped by men in the Portuguese colonies, also producing extramarital children (Smith, 1997). The fact that the polygynous males in the New World Iberian colonies were usually Europeans, who were the most socially privileged, is in agreement with patterns from most other societies, in which, when polygyny existed, it tended to be with men in the upper classes (Betzig, 1993). As in most other societies, rape of low-status women by high-status men was more common than the reverse. For example, more Black women were raped by White men before the civil rights movement of the 1950s and 1960s in the United States than White women were by Black men (Dorr, 2004; McGuire, 2011).

The role of assortative mating in patterns of parenting. The phenomenon of assortative mating needs to be considered as a final factor of importance to population genetics. Assortative mating is defined as the disproportionate mating of individuals who are phenotypically and genetically similar, suggesting that the traits in question are heritable. Although mating and gene flow are usually considered stochastic processes in population genetics, human mating is almost never random. Humans are geographically constrained by whom they can mate with based on proximity, geography, cultural norms and values, and other factors that then shape mating patterns. A large body of research supports the idea that individuals do not select mates stochastically but instead mate assortatively, utilizing "phenotypic similarity to guide mate choice" (Buss & Barnes, 1986; Jobling et al., 2013, p. 611). Reports suggest that humans mate assortatively for various traits—including age, previous marital

status, religion, SES, ethnicity, height, hair and eye color, psychological traits, and physical attractiveness (Buss & Barnes, 1986; Vandenberg, 1972).

Several evolutionary principles are thought to govern the process of assortative mating. *Kin selection theory* (Hamilton, 1963) posits that organisms are more likely to assist organisms that are genetically related *or* genetically similar to increase *inclusive fitness*—the amount of offspring an organism has *and* the amount genetically related kin have. According to *genetic similarity theory* (Rushton, 1989), assortative mating provides the mechanism through which individuals seek to find mates possessing a high level of phenotypic similarity. Highly similar individuals should share a higher proportion of genes than would be expected by chance, making the next generation of organisms higher in genetic similarity to the parents, thus promoting higher levels of parental investment (Figueredo & Wolf, 2009).

Another relevant evolutionary principle is *group selection*, which is construed within the broader framework of *multilevel selection theory* (e.g., Hertler et al., 2020), in that the phenomenon of Dutton's rule might be considered to represent the action of Type 1 group selection (Okasha, 2006), in which the benefits of group competition accrue to the relative as well as the aggregate fitness of the individuals within the winning group.

This raises the question of what happens to parental investment in modern Latin America, where society is composed primarily of individuals with ethnically mixed ancestry. One solution to this paradox is the finding that individuals in mixed-ethnicity populations assortatively mate for features other than ethnicity that have been demonstrated to be important in assortative mate choice and highly heritable (Rushton, 1989). The rationale is that mixed-ancestry individuals will overcompensate in similarity in other dimensions of mate choice, as ethnicity is dissimilar. Another answer is that mixed-ethnicity individuals use genetic similarity "detectors" (innate feature detectors, familiarity or association, and location, kin recognition) to detect the proportion of ancestry each possesses.

Risch and colleagues (2009) argued that "proximal traits" would be appropriate for ancestrally homogeneous groups, but they may not work as well in heterogeneous populations. In their study, Risch and a group of researchers sampled Latin American populations from four sites—San Francisco, New York, Mexico City, and Puerto Rico—and tested them for ancestry-informative genetic markers. The results showed that Mexican populations (San Francisco and Mexico City) mated

assortatively for European and indigenous ancestry, while Puerto Rican populations (New York and Puerto Rico) mated assortatively for degrees of European and African ancestry. Spouses shared equal proportions of genetic ancestry—there were no significant differences between husbands and wives in the four locations. Though this may be evidence of genetic similarity detectors, Risch and colleagues argue that this may be an effect of assortative mating based on social strata—something we will revisit in future directions of our paper.

We might conclude, therefore, that assortative mating patterns did not disfavor parental investment as much as might have been supposed in the ethnically hybridized populations of Latin America. Indeed, recent empirical evidence indicates that a sample of northern Mexicans scored comparably in levels of total parental effort and shared parenting to a sample of non-Hispanic residents of the southwestern United States (Sotomayor et al., 2013).

Disease, differential mortality, and selection

An important element in understanding ethnic admixture in Latin America is the question of the resistance to both New World and Old World pathogens that it might provide. Therefore, we examine the role that epidemic diseases might have played in the history of interethnic relations after the Columbian Exchange. This includes not only the diseases introduced by European colonists to the indigenous peoples but also those contracted by the same colonists upon contact with the latter.

On top of the harsh policies of exploitation of indigenous cultures, European immigrants inadvertently brought transmissible pathogens that were novel to the Americas, including measles, influenza, scarlet and typhoid fever, typhus, pertussis, tuberculosis, cholera, diphtheria, chickenpox, and some sexually transmitted diseases, causing widespread epidemics that killed millions of Amerindians (Waldman, 2009). The slave trade also brought yellow fever and other diseases to the Americas from Africa (Oldstone, 2009; Chippaux & Chippaux, 2018). Some of the diseases that affected Amerindians upon the arrival of Europeans are likely to have already existed among the Amerindian populations, such as tuberculosis (Bos et al., 2014) and peptic ulcer disease (Domínguez-Bello et al., 2008); however, new strains were also introduced to the native populations, and European and African strains were able to expand their range over native strains because of the lower genetic diversity of the latter (Domínguez-Bello et al., 2008).

Some Amerindian tribes neared extinction as a result of the destructive spread of diseases (Waldman, 2009). The Arawak peoples of the Caribbean, who were subjugated and enslaved by Columbus, are estimated to have had a precontact population of 8 million people that subsequently dwindled to approximately 3 million, mainly from epidemics; Timucuans lost 98% of their population (Calloway, 1997, p. 33; Churchill, 1997; Skidmore & Smith, 2005). In Mexico, prior to the arrival of Spanish conquistadors, the population of natives was estimated to be 25 million inhabitants; by 1605, the native population had dwindled to 1 million inhabitants (Skidmore & Smith, 2005).

Again, experts cite disease as a major contributor to declining native populations. Because epidemics had been present in Europe, most European adults had experienced immunity to diseases, although younger children were at risk of mortality. The natives in the Americas, however, never having been subjected to these diseases, were not inoculated and perished at all ages in the lifespan (Skidmore & Smith, 2005; Thomson, 1998). The transmission of novel diseases occurred mainly through Indian routes designated for trade and commerce, where diseases migrated from infected natives to distant native neighbors—sometimes with little direct contact with Europeans—destroying areas in Mexico, Peru, and the Yucatan, among others (Calloway, 1997; Thomson, 1998). The impact of slavery, warfare, and disease was pervasive in Amerindian culture. Tribes that were once solidified by tribal elders and kin cohesion experienced a loss of members and leaders, leading to "a weakening of the social structure" (Thomson, 1998, p. 122) and leaving native culture penetrable to Christian influence (Calloway, 1997; Skidmore & Smith, 2005).

It must also be noted that the distribution of European DNA in North and South America with respect to Amerindian and African DNA has been substantially influenced by local ecologic forces. In American countries located south of the equator, the average percentage of European-ancestry alleles possessed by the population is greater further to the south (e.g., Callegari-Jacques et al., 2003), whereas in American countries north of the equator, the reverse tends to be true (e.g., Moreno-Estrada et al. 2014), with correlations between territory latitude and average percentage of European ancestry being very high (~ $r = .90$). This genetic trend may be associated with the biogeography of parasite diversity and the ecological dynamics of new diseases introduced to the American territories during colonization: it is well known that tropical latitudes favor higher parasite

transmission, promoting higher parasite diversity in humans and other mammals (e.g., Bordes et al., 2010; Guernier et al., 2004). European settlers suffered and a staggeringly high number of them perished from local diseases and from diseases brought by African slaves in more tropical regions of America, such as outbreaks of yellow fever in the Caribbean in the seventeenth to the nineteenth centuries (Oldstone, 2009; Watts, 2001), malaria, and tuberculosis (Acemoglu et al., 2003; Yalcindag et al., 2012), making these regions practically impossible for Europeans to successfully settle.

Adaptive introgressions

It has recently been proposed that the so-called Columbian Exchange of people, plants, and parasites occasioned a process of *adaptive introgression* in New World human populations (Jordan, 2016). Adaptive introgression is a process that begins with hybridization among two or more nascent species or subspecies that previously had been reproductively and perhaps geographically isolated but subsequently came into contact. Adaptive introgression, however, goes beyond simple hybridization in that subsequent selection differentially filters the introgressed genes according to their adaptive consequences. Thus, the genes that are successfully selected come to exist at more than chance levels in the hybridized population, as they presumably confer advantages in survival and reproduction (Martinsen et al., 2001; Hamilton & Miller, 2016; Hedrick, 2013; Twyford & Ennos, 2012). This kind of analysis has not been carried out exhaustively with hybridized New World human populations, but some early results indicate that some African MHC (major histocompatibility complex) genes are statistically overrepresented that probably confer resistance to infectious diseases (Zhou et al., 2016).

Despite the hard genetic evidence required to conclusively establish the occurrence of adaptive introgression in hybridized New World human populations, the phenomenon is quite well documented in biology in a diverse array of other taxa. For example, evidence for adaptive introgression has been reported for certain mimetic adaptations in *Heliconius* butterflies (Pardo-Díaz et al., 2012); for the adaptive radiation of certain *Cyprinodon* pupfishes across geographically distant Caribbean islands (Richards & Martin, 2017; Gerber et al., 2001); for insecticide resistance in certain *Anopheles* malarial mosquitoes (Norris et al., 2015); for anticoagulant rodent poison resistance in Old World *Mus* house

mice (Song et al., 2011; Rieseberg, 2011); for social, sexual, and parental behavior in *Zonotrichia* sparrows (Tuttle et al., 2016); for increased body size in altered habitats in *Ambystoma* tiger salamanders (Fitzpatrick & Shaffer, 2007; Fitzpatrick et al., 2010); for increased body size and skeletal proportions that facilitate hunting larger prey in North American *Canis* coyote-wolf hybrids (vonHoldt et al., 2016); for pigmentary diversity in North American forested habitats among *Canis* wolf-dog hybrids (Anderson et al., 2009); for increased maturational speed and sexually selected features in Amboseli basin *Papio* yellow-anubis baboon hybrids (Charpentier et al., 2008; Charpentier et al., 2012; Tung et al., 2012); and for pistil self-incompatibility specificity in *Arabidopsis* mustard weeds (Castric et al., 2008).

There is a growing corpus of evidence that modern human populations contain adaptive introgressions from several archaic human populations, including Neanderthals and Denisovans (Racimo et al., 2016). For example, evidence for adaptive introgression has been reported for altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA (Huerta-Sanchez et al., 2014; Huerta-Sanchez & Casey, 2015). A similar effect has been found among Peruvians living at high altitudes (Gonzáles, 2007). Although all the evidence is not yet in for adaptive introgressions in hybridized New World human populations, we do not believe it is much of a reach to contemplate the working hypothesis that such a combination of admixture plus selection shaped the modern populations of Latin America.

Health and evolutionary implications of admixture

Genetic diversity, influenced by European colonization, is an important biological variable with direct implications for disease vulnerability and indirect implications for social dynamics. Genetic diversity is defined as the magnitude of genetic variability within a population, measured by the average degree of heterozygosity across loci, allelic diversity, haplotype diversity, and other related metrics (Hughes et al., 2008). Amerindians have been found to have lower degrees of heterozygosity than populations from other geographic regions (around 12% to 22% less than Europeans and 16% to 25% less than Africans) and fewer distinct alleles per locus compared with populations on other continents (around 15% fewer alleles per locus than Europeans and 25% fewer than Africans; Wang et al., 2007). In some studies, the contrast is even more striking: a 1.75-fold range in

nucleotide heterozygosity has been found, with West African genomes being the most diverse and certain Native American genomes being the least diverse (e.g., Kidd et al., 2012).

Genetic diversity in native populations is purported to be lower as their distance from the Bering Strait increases because of genetic bottlenecks that occurred during ancient migrations, mainly from north to south in the Americas (Wang et al., 2007). Thus, Latin American populations present even less diversity than Native Americans from the United States and Canada (Wang et al., 2007). Admixed Latin American populations have higher genetic diversity than Amerindian populations (Rangel-Villalobos et al., 2000), and the degree of genetic diversity in the former is a positive function of the degree of European admixture (Wang et al., 2008). Still, even admixed Latin American populations appear to have lower genetic diversity on average than populations from other continents already examined, based on haplotype diversity (Silva-Zolezzi et al., 2009).

Genetic diversity in Latin America has also increased across the centuries as a result of the complex patterns of African slavery and European migration. The complexity is both geographic (in terms of origins) and temporal (in terms of when populations were introduced to Latin America; Ongaro et al., 2019). Between the sixteenth and nineteenth centuries, the bulk of efforts shifted several times from one region of Africa to another for the extraction of slaves brought to Latin America, mainly through four cycles that concentrated, initially, on coastal regions of Western sub-Saharan Africa, such as Guinea, Angola, and the Benin-Dahomey stretch, and subsequently on more inland and Eastern regions, such as Mozambique (Bueno, 2003). Different African populations were used as slaves across time, with cumulative ethnic diversity being introduced to Latin America.

This increasing diversity across centuries can also be observed in the case of European migration, which was initially of predominantly Iberian origin and subsequently of mostly Italian and German origins to certain Latin American regions, such as Argentina (Fausto, 1999). Cutting-edge evidence has been presented of important genomic proportions of Jewish and Middle Eastern groups in several Latin American countries (Ongaro et al., 2019). This pattern of genetic diversity has resulted in substantial heterogeneity among Latino groups (Conomos et al., 2016). The genetic divergence and complexity among Latin American populations was compounded by the occurrence of both pre- and

postcolonization genetic bottlenecks (perhaps a result of founder effects) identified in several Latin American populations (Belbin et al., 2018). Such bottlenecks generated localized genetic patterns.

Populational genetic diversity has been demonstrated to be negatively associated with disease vulnerability and with invasibility (vulnerability to have territories and ecologies invaded and even taken over by other populations or by other species), and it is positively associated with population recovery from disturbance and with evolutionary potential to respond to novel selection pressures (for a review, see Hughes et al., 2008). It is thus logical to imagine that the low genetic diversity of Amerindian populations facilitated European expansion in the Americas. Moreover, as limited genetic diversity of hosts limits the diversity of colonizing species, it has been predicted that Amerindian strains of parasites are the least diverse. This has been tested and corroborated with *Helicobacter pylori* (Domínguez-Bello et al., 2008). All strains that were cultured from native Africans were African strains, all from the Spanish were European strains, and all from Koreans were East Asian strains; however, mestizos (from Colombia and Venezuela) carried African and European strains only, while Amerindians carried European and Amerindian strains (which were found to be less diverse than European and African).

An important effect of the historical admixture in Latin America is the dilution of deleterious alleles. Alleles related to predisposition or to vulnerability to diseases are often different among human continental populations (Burchard et al., 2003), and a consequence of the European colonization and the introduction of African slaves is that the resultant hybrid populations are expected to have disease prevalences (e.g., Mendelian disorders) that are intermediate between those of the ancestral populations (Jobling et al., 2013). Moreover, admixture is expected to reduce the disease burden of invaded and invader populations, compared with the initial high levels of morbidity and mortality resulting from the transmission of population-specific pathogens from invaders to invaded and vice versa. For example, recent evidence suggests that the prevalence of multiple sclerosis is comparatively low in Latin America, and especially lower in regions of more intense admixture (for a review, see Negrotto & Correale, 2018). Genetic variants that appear to be protective against this neurological disorder, which are rare or absent in European and African populations, are retained in high frequency in admixed populations in Latin America (Aguirre-Cruz et al., 2011; Cristiano et al., 2013). The frequent exposure

to diverse and novel pathogens that characterized this region historically also appears to serve as a protective factor against the development of multiple sclerosis, and against relapses, as seems to also be the case in a variety of other autoimmune diseases (Negrotto & Correale, 2018).

Selective pressures are expected to result in an admixed population with a substantial bias toward contributions from the population that is more resistant (Jobling et al., 2013). In the first couple of generations after the onset of admixture, this bias is expected to extend toward all loci regardless of the degree to which they are linked to the loci conferring disease resistance; however, in later generations, this bias is expected to be limited to linked loci, as the admixture patterns become increasingly fragmented across the genome (Jobling et al., 2013). HLA alleles are an example of this phenomenon: among Puerto Ricans, there is an "excess" of African ancestry and a "deficiency" of European ancestry relative to the expectation based on genome-wide averages (Tang et al., 2007), indicating an adaptive advantage of the African alleles in Puerto Ricans. The reason we believe that African HLA alleles would be more advantageous than European HLA alleles in Puerto Rico is that Puerto Rico has a subtropical climate and thus a higher parasite burden than the temperate climates of Europe. In addition, certain African diseases (e.g., malaria and yellow fever) were imported to Puerto Rico by the slave trade (e.g., Chippaux & Chippaux, 2018; Yalcindag et al., 2012), and we believe it is logical to assume that African HLA alleles will confer greater resistance to the same than European ones (see Rotimi et al., 2016, for a discussion of the health implications of admixture from the African diaspora).

The existence of such examples and the fact that a very high percentage of individuals in Latin America are admixed permit us to conclude that admixture between the three main ethnic categories that have made up Latin American populations in the last five centuries have resulted not simply in heterosis due to masking of genetic load, as the benefits of this diminish over generations, but rather in increases in mean population fitness that have been maintained over time, which can be mainly be attributable to two mechanisms: (1) increases in the admixed populations relative to non-admixed populations in the evolutionary potential to respond to novel selection pressures, as a result of the higher genetic diversity propitiated by the admixture; and (2) recombination and segregation of unique phenotypes among the progeny that may be favored by selection (Keller & Taylor, 2010).

Limitations of the study

Admittedly, our entire thesis is based on broad generalizations regarding the dynamics of the postcontact genetic and microbial exchanges between indigenous Native Americans and European colonists. We understand that it might have been an outstanding achievement to provide a more detailed account of the interactions between each individual indigenous culture and each individual colonizing European subgroup. Nevertheless, that could only be accomplished comprehensively by a nineteenth-century style treatise spanning many volumes of elaborate description; it simply cannot be contained within the confines of a contemporary journal article. As a consequence of this limitation, we have instead proposed a general theory that sacrifices a finer-grained level of detail for greater scope of applicability.

As an intellectual reaction to the perceived ethnocentrism of early evolutionary theories of culture (e.g., Morgan, 1877) that were based on proposed universal laws using *nomothetic* approaches, the Boasian School of cultural anthropology introduced the concept of *historical particularism* (e.g., Boas, 1896), which advocated that cultures be studied instead on case-by-case basis using *idiographic* approaches (Harris, 1968; Langness, 1974). This alternative view eschewed the notion that some cultures were more evolved than others, as with Morgan's (1877) proposed progression from *savagery* through *barbarism* to *civilization*.

Although the approach of historical particularism has demonstrated its worth in an efflorescence of detailed ethnographic studies of specific cultures, we do not believe that its judicious application completely invalidates the value of drawing cautious generalizations from the data, especially when no ethnocentric intent is implied. Indeed, a rational balance between the particular and the general level of description is the basis for the entire science of taxonomy. For example, there are an estimated 5,416 of mammals (Burgin et al., 2018) and a newly estimated 18,043 species of birds worldwide (Barrowclough et al., 2016). Each of these individual species possesses its own unique natural history, ecology, phylogeny, biology, and behavior. Nevertheless, this does not prevent taxonomists from asserting that all birds have feathers and that all mammals do not or that all female mammals have mammary glands for nursing their young and that all birds do not. The entire list of systematic differences between these large-scale taxonomic categories is quite large, in spite of the otherwise prodigious diversities within them.

Similarly, we maintain that there is some validity to making generalizations that compare certain key characteristics of the aboriginal Americans with those of the invasive European colonists. For example, although it is hard to document a negative, there is no evidence that any particular aboriginal American groups were especially resistant to European-introduced diseases such as bubonic plague, measles, smallpox, mumps, chickenpox, influenza, cholera, diphtheria, typhus, malaria, leprosy, or yellow fever (Martin & Goodman, 2002), making these classifiable as "virgin soil epidemics" (Crosby, 1976). In spite of purely cultural diversity, there is a robust finding from all lines of evidence (e.g., mtDNA, Y-chromosomal DNA, and autosomal DNA) generally reporting a relatively low degree of genetic diversity among Native Americans (Mulligan et al., 2004) compared with other human groups, rendering such purely biological generalizations more viable. Correspondingly, there were many commonalities among the European colonists that had important consequences (Diamond, 2005).

In summary, we believe that we are justified in making certain generalizations regarding these broader groups and the interactions between them, in the service of developing a general theory describing the dynamics of the postcontact genetic and microbial exchanges between them, in spite of the acknowledged diversities within them.

Consequently, we do not address the development and diversification of contemporary Latin American cultural identities, which would be beyond the scope of this article and our realms of expertise. Further, we make no claim that the factors that we explicitly address (i.e., genetic and microbial exchange) solely or even mostly determine Latino cultural identities. Readers who are interested in those sociological issues are directed to the extensive and rich literature that explores the political, ideological, and public health implications of ethnic and cultural identity (García-Deister & López-Beltrán, 2015; Morera et al., 2003; Vasquez & Deister, 2019; Wade, 2017a; Wade et al., 2014).

Conclusions

The present article sought to link historical evidence and evolutionary mechanisms with extant literature documenting the pattern of genetic admixture present in modern Latin America. Because the intermingling and interbreeding of distinct populations is rapidly occurring at a global level, the insights derived from exploring Latin America as a case study for admixture may provide

larger-scale insights for researchers interested in cultural and social dynamics. It has long been recognized that Amerindians, Europeans, and Africans exchanged infectious diseases during the colonization of the Americas, leading to widespread epidemics within Amerindian populations. Possible reasons for these events were examined and the relevance regarding the differences in population-genetic diversity between Amerindians and other groups were discussed in regard to the understanding of the historical interplay between the colonization of the New World and the health of its populations. Central to this is the recognition that Amerindian populations present lower genetic diversity than most other ethnic groups, leading to greater disease vulnerability and thus greater vulnerability to have territories invaded.

Second, we discussed how the historical interethnic admixture in Latin America led to the dilution of deleterious alleles related to vulnerability to diseases and created a buffer against further decimation of Amerindian populations.

Third, we discussed how the ecology of infectious diseases needs to be taken into consideration when studying the colonization of America and its fitness consequences, as microbial diversity and transmission is heightened in tropical compared with temperate zones.

Finally, we reviewed the consequences of historical racial oppression and unequal distribution of resources in Latin American history to the health of Amerindians and their living conditions and proposed interplays between these social and the genetic and evolutionary causes of health differences between Amerindians, mestizos, and Europeans.

References

Acemoglu, D., Johnson, S., & Robinson, J. (2003). Disease and development in historical perspective. *Journal of the European Economic Association*, 1(2–3), 397–405. https://doi.org/10.1162/154247603322391035

Adams, R. N. (2005). Etnicidad e igualdad en Guatemala 2002 [Ethnicity and equality in Guatemala 2002]. *Serie Políticas Sociales*, No. 107. Comisión Económica para América Latina y el Caribe (CEPAL). https://repositorio.cepal.org/handle/11362/6101

Adhikari, K., Chacón-Duque, J. C., Mendoza-Revilla, J., Fuentes-Guajardo, M., & Ruiz-Linares, A. (2017). The genetic diversity of the Americas. *Annual Review of Genomics and Human Genetics*, 18, 277–296. https://doi.org/10.1146/annurev-genom-083115-022331

Adhikari, K., Mendoza-Revilla, J., Chacón-Duque, J. C., Fuentes-Guajardo, M., & Ruiz-Linares, A. (2016). Admixture in Latin America. *Current Opinion in Genetics & Development*, 41, 106–114. http://doi.org/10.1016/j.gde.2016.09.003

Adler, N. E., & Stewart, J. (2010). Health disparities across the lifespan: Meaning, methods, and mechanisms. *Annals of the New York Academy of Sciences*, 1186, 5–23. https://doi.org/10.1111/j.1749-6632.2009.05337.x

Aguirre-Cruz, L., Flores-Rivera, J., De La Cruz-Aguilera, D. L., Rangel-López, E., & Corona, T. (2011). Multiple sclerosis in Caucasians and Latino Americans. *Autoimmunity*, 44(7), 571–575. https://doi.org/10.3109/08916934.2011.592887

Alcock, J. (2009). *Animal behavior: An evolutionary approach* (9th ed.). Sinauer.

Algee-Hewitt, B. F. B., & Goldberg, A. (2016). Better together: Thinking anthropologically about genetics. *American Journal of Physical Anthropology*, 160(4), 557–560. https://doi.org/10.1002/ajpa.23022

Ali, Y. (2012). Shariah and citizenship—How Islamophobia is creating a second-class citizenry in America. *California Law Review*, 100(4), 1027–1068. https://doi.org/10.15779/Z38481V

Anderson, T. M., vonHoldt, B. M., Candille, S. I., Musiani, M., Greco, C., Stahler, D. R., Smith, D. W., Padhukasahasram, B., Randi, E., Leonard, J. A., Bustamante, C. D., Ostrander, E. A., Tang, H., Wayne, R. K., & Barsh, G. S. (2009). Molecular and evolutionary history of melanism in North American gray wolves. *Science*, 323(5919), 1339–1343. https://doi.org/10.1126/science.1165448

Antón, J., Bello, Á., Del Popolo, F. Paixao, M., & Rangel, M. (2009). Afrodescendientes en América Latina y el Caribe: Del reconocimiento estadístico a la realización de derechos [Afro-descendants in Latin America and the Caribbean: From the statistical recognition to the realization of rights]. Serie Población y Desarrollo No. 87. Comisión Económica para América Latinay el Caribe (CEPAL). https://repositorio.cepal.org/handle/11362/7227

Aoki, K. (2002). Sexual selection as a cause of human skin colour variation: Darwin's hypothesis revisited. *Annals of Human Biology*, 29(6), 589–608. https://doi.org/10.1080/0301446021000019144

Balaresque, P., Bowden, G. R., Adams, S. M., Leung, H. Y., King, T. E., Rosser, Z. H., Goodwin, J., Moisan, J. P., Richard, C., Millward, A., Demaine, A. G., Barbujani, G., Previderè, C., Wilson, I. J., Tyler-Smith. C., & Jobling. M. A. (2010). A predominantly Neolithic origin for European paternal lineages. *PLOS Biology*, 8(1), e1000285. https://doi.org/10.1371/journal.pbio.1000285

Barrowclough, G. F., Cracraft, J., Klicka, J., & Zink, R. M. (2016). How many kinds of birds are there and why does it matter? *PLOS ONE*, 11(11), e0166307. https://doi.org/10.1371/journal.pone.0166307

Bastide, R. (1974). The present status of Afro-American research in Latin America. *Daedalus*, 103(2), 111–123.

Basu, A., Sarkar-Roy, N., & Majumder, P. P. (2016). Genomic reconstruction of the history of extant populations of India reveals five distinct ancestral components and a complex structure. *Proceedings of the National Academy of Sciences*, 113(6), 1594–1599. https://doi.org/10.1073/pnas.1513197113

Bateman, A. J. (1948). Intra-sexual selection in *Drosphilia*. *Heredity*, 2, 349–368. https://doi.org/10.1038/hdy.1948.21

Bedoya, G., Montoya, P., García, J., Soto, I., Bourgeois, S., Carvajal, L., Labuda, D., Alvarez, V., Ospina, J., Hedrick, P. W., & Ruiz-Linares, A. (2006). Admixture dynamics in Hispanics: A shift in the nuclear genetic ancestry of a South American population isolate. *Proceedings of the National Academy of Sciences*, 103(19), 7234–7239. https://doi.org/10.1073/pnas.0508716103

Belbin, G. M., Nieves-Colón, M. A., Kenny, E. E., Moreno-Estrada, A., & Gignoux, C. R. (2018). Genetic diversity in populations across Latin America: Implications for population and medical genetic studies. *Current Opinion in Genetics & Development*, 53, 98–104. https://doi.org/10.1016/j.gde.2018.07.006

Berniell-Lee, G., Calafell, F., Bosch, E., Heyer, E., Sica, L., Mouguiama-Daouda, P., van der Veen, L., Hombert, J. M., Quintana-Murci, L., & Comas, D. (2009). Genetic and demographic implications of the Bantu expansion: Insights from human paternal lineages. *Molecular Biology and Evolution*, 26(7), 1581–1589. https://doi.org/10.1093/molbev/msp069

Betzig, L. (1993). Sex, succession, and stratification in the first six civilizations: How powerful men reproduced, passed power on to their sons, and used power to defend their wealth, women, and children. In E. Lee (Ed.). *Social stratification and socioeconomic inequality* (Vol. 1, pp. 37–74). Praeger.

Bird, Y., Staines-Orozco, H., & Moraros, J. (2016). Adolescents' smoking experiences, family structure, parental smoking and socio-economic status in Ciudad Juárez, Mexico. *International Journal for Equity in Health*, 15, 29. https://doi.org/10.1186/s12939-016-0323-y

Boas, F. (1896). The limitations of the comparative method of anthropology. *Science*, 4(103), 901–908. http://doi.org/10.1126/science.4.103.901

Bokek-Cohen, Y., Peres, Y., & Kanazawa, S. (2008). Rational choice and evolutionary psychology as explanations for mate selectivity. *Journal of Social, Evolutionary, and Cultural Psychology*, 2(2), 42–55. https://doi.org/10.1037/h0099356

Bordes, F., Morand, S., Krasnov, B.R., & Poulin, R. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. In S. Morand and B. R. Krasnov (Eds.), *The biogeography of host-parasite interactions* (pp. 89–98). Oxford University Press.

Bortolini, M. C., Da Silva, W. A., De Guerra, D. C., Remonatto, G., Mirandola, R., Hutz, M. H., Silva, M. C., Zago, M. A., & Salzano, F. M. (1999). African-derived South American populations: A history of symmetrical and asymmetrical matings according to sex revealed by bi- and uni-parental genetic markers. *American Journal of Human Biology*, 11(4), 551–563. https://doi.org/10.1002/(SICI)1520-6300(1999)11:4>551::AID-AJHB15>3.0.CO;2-Z

Bos, K. I., Harkins, K. M., Herbig, A., Coscolla, M., Weber, N., Comas, I., Forrest, S. A., Bryant, J. M., Harris, S. R., Schuenemann, V. J., Campbell, T. J., Majander, K., Wilbur, A. K., Guichon, R. A., Steadman, D. L. W., Cook, D. C., Niemann, S., Behr, M. A., Zumarraga, M., . . . Krause, J. (2014). Pre-Columbian mycobacterial genomes reveal seals as a source of New World human tuberculosis. *Nature*, 514, 494–497. https://doi.org/10.1038/nature13591

Brissenden, J. E., Kidd, J. R., Evsanaa, B., Togtokh, A. J., Pakstis, A. J., Friedlaender, F., Kidd, K. K., & Roscoe, J. M. (2015). Mongolians in the genetic landscape of Central Asia: Exploring the genetic relations among Mongolians and other world populations. *Human Biology*, 87(2), 73–91. https://doi.org/10.13110/humanbiology.87.2.0005

Bryc, K., Velez, C., Karafet, T., Moreno-Estrada, A., Reynolds, A., Auton, A., Hammer, M. H., Bustmante, C. D., & Ostrer, H. (2010). Genome-wide patterns of population structure and admixture among Hispanic/Latino populations. *Proceedings of the National Academy of Sciences*, 107, 8954–8961. https://doi.org/10.1073/pnas.0914618107

Bueno, E. (2003). *Brasil: Uma história*. Ática.

Burchard, E. G., Ziv, E., Coyle, N., Gomez, S. L., Tang, H., Karter, A. J., Mountain J. L., Pérez-Stable, E. J., Sheppard. D., & Risch, N. (2003). The importance of race and ethnic background in biomedical research and clinical practice. *New England Journal of Medicine*, 348(12), 1170–1175. http://doi.org/10.1056/NEJMsb025007

Burgin, C. J., Colella, J. P., Kahn, P. L., & Upham, N. S. (2018). How many species of mammals are there? *Journal of Mammalogy*, 99(1), 1–14. https://doi.org/10.1093/jmammal/gyx147

Burrows, N. R., Geiss, L. S., Engelgau, M. M., & Acton, K. J. (2000). Prevalence of diabetes among Native Americans and Alaska Natives, 1990–1997: An increasing burden. *Diabetes Care*, 23(12), 1786–1790. https://doi.org/10.2337/diacare.23.12.1786

Buss, D. M. (1989). Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12(1), 1–49. https://doi.org/10.1017/S0140525X00023992

Buss, D. M., & Barnes, M. (1986). Preferences in human mate selection. *Journal of Personality and Social Psychology*, 50(3), 559–570. https://doi.org/10.1037/0022-3514.50.3.559

Cabeza de Baca, T., Sotomayor-Peterson, M., Smith-Castro, V., & Figueredo, A. J. (2014). Contributions of matrilineal and patrilineal kin alloparental effort to the development of life history strategies and patriarchal values: A cross-cultural life history approach. *Journal of Cross Cultural Psychology*, 45(4), 534–554. https://doi.org/10.1177%2F0022022113513068

Callegari-Jacques, S. M., Grattapaglia, D., Salzano, F. M., Salamoni, S. P., Crossetti, S. G., Ferreira, M. E., & Hutz, M. H. (2003). Historical genetics: Spatiotemporal analysis of the formation of the Brazilian population. *American Journal of Human Biology*, 15(6), 824–834. https://doi.org/10.1590/1678-4685-gmb-2018-0076

Calloway, C. G. (1997). *New worlds for all: Indians, Europeans, and the remaking of early America*. John Hopkins University Press. https://doi.org/10.1080/03612759.1998.10528104

Cameron, E. Z., & Dalerum, F. (2009). A Trivers-Willard effect in contemporary humans: male-biased sex ratios among billionaires. *PLoS One*, 4(1), e4195. https://doi.org/10.1371/journal.pone.0004195

Candelaria, C. (1980). La Malinche, feminist prototype. *Frontiers: A Journal of Women Studies*, 5(3), 1–6.

Carvajal-Carmona, L. G., Ophoff, R., Hartiala, J., Molina, J., Leon, P., Ospina, J., Bedoya, G., Freimer, N., & Ruiz-Linares, A. (2003). Genetic demography of Antioquia (Colombia) and the central valley of Costa Rica. *Human Genetics*, 112, 534–541. https://doi.org/10.1007/s00439-002-0899-8

Cashdan, E. (1996). Women's mating strategies. *Evolutionary Anthropology*, 5(4), 134–143. https://doi.org/10.1002/(SICI)1520-6505(1996)5:4%3C134::AID-EVAN3%3E3.0.CO;2-G

Castric, V., Bechsgaard, J., Schierup, M. H., & Vekemans, X. (2008). Repeated adaptive introgression at a gene under multiallelic balancing selection. *PLOS Genetics*, 4(8), e1000168. https://doi.org/10.1371/journal.pgen.1000168

Chakraborty, R. (1986). Gene admixture in human populations: Models and predictions. *Yearbook of Physical Anthropology*, 29, 1–43. https://doi.org/10.1002/ajpa.1330290502

Charpentier, M. J. E, Fontaine, M. C., Cherel, E., Renoult, J. P., Jenkins, T., Benoit, L., Barthès, N., Alberts. S. C., & Tung, J. (2012). Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population. *Molecular Ecology*, 21(3), 715–731. https://doi.org/10.1111/j.1365-294X.2011.05302.x

Charpentier, M. J. E., Tung, J., Altmann, J., & Alberts, S. C. (2008). Age at maturity in wild baboons: genetic, environmental and demographic influences. *Molecular Ecology*, 17(8), 2026–2040. https://doi.org/10.1111/j.1365-294X.2008.03724.x

Chasteen, J. C. (2004). *Born in blood and fire: A concise history of Latin America* (2nd ed.). W. W. Norton & Co.

Chiaroni, J., King, R. J., Myres, N. M., Henn, B. M., Ducourneau, A., Mitchell, M. J., Boetsch, G., Sheikha, I., Lin, A. A., Nik-Ahd, M., Ahmad, J., Lattanzi, F., Herrera, R. J., Ibrahim, M. E., Brody, A., Semino, O., Kivisild, T., & Underhill, P. A. (2010). The emergence of Y-chromosome haplogroup J1e among Arabic-speaking populations. *European Journal of Human Genetics*, 18(3), 348–353. https://doi.org/10.1038/ejhg.2009.166

Chikhi, L., Nichols, R. A., Barbujani, G., & Beaumont, M. A. (2002). Y genetic data support the Neolithic demic diffusion model. *Proceedings of the National Academy of Sciences*, 99 (17), 11008–11013. https://doi.org/10.1073/pnas.162158799

Chippaux, J.-P., & Chippaux, A. (2018). Yellow fever in Africa and the Americas: A historical and epidemiological perspective. *Journal of Venomous Animals and Toxins including Tropical Diseases*, 24, 20. https://doi.org/10.1186/s40409-018-0162-y

Churchill, W. (1997). *A little matter of genocide: Holocaust and denial in the Americas: 1492 to the present*. City Lights Books.

Cochran, G., & Harpending, H. (2010). *The 10,000 year explosion: How civilization accelerated human evolution*. Basic Books.

Comisión Económica para América Latina y el Caribe (CEPAL). (2014). *Los pueblos indígenas en América Latina: avances en el último decenio y retos pendientes para la garantía de sus derechos* [Indigenous peoples in Latin America: Progress in the last decade and pending challenges to guarantee their rights]. https://repositorio.cepal.org/handle/11362/37050

Conomos, M. P., Laurie, C. A., Stilp, A. M., Gogarten, S. M., McHugh, C. P., Nelson, S. C., Sofer, T., Fernández-Rhodes, L., Justice, A. E., Graff, M., Young, K. L., Seyerle, A. A., Avery, C. L., Taylor, K. D., Rotter, J. I., Talavera, G. A., Daviglus, M. L., Wassertheil-Smoller, S., . . . Laurie, C. C. (2016). Genetic diversity and association studies in US Hispanic/Latino populations: Applications in the Hispanic Community Health Study/Study of Latinos. *American Journal of Human Genetics*, 98(1), 165–184. https://doi.org/10.1016/j.ajhg.2015.12.001

Costa, M. D., Pereira, J. B., Pala, M., Fernandes, V., Olivieri, A., Achilli, A., Perego, U. A., Rychkov, S., Naumova, O., Hatina J., Woodward, S. R., Eng, K. K., Macaulay, V., Carr, M., Soares, P., Pereira, L., & Richards, M. B. (2013). A substantial prehistoric European ancestry amongst Ashkenazi maternal lineages. *Nature Communications*, 4, 2543. https://doi.org/10.1038/ncomms3543

Cristiano, E., Rojas, J. I., Romano, M., Frider, N., Machnicki, G., Giunta, D. H., Calegaro. D., Corona, T., Flores, J., Gracia, F., Macias-Islas, M., & Correale, J. (2013). The epidemiology of multiple sclerosis in Latin America and the Caribbean: A systematic review. *Multiple Sclerosis Journal*, 19(7), 844–854. https://doi.org/10.1177/1352458512462918

Crosby, A. W., Jr. (1976). Virgin soil epidemics as a factor in the aboriginal depopulation in America. *William and Mary Quarterly*, 33(2), 289–299. http://doi.org/10.2307/1922166

Davis M.F., Guggenheim, C., Figueredo, A.J., Wright, A., & Locke, C. (2007). Differential parental investment in Tucson babies. *Journal of the Arizona Nevada Academy of Science*, 39 (2), 65–72.

Dawkins, R. (2004). Extended phenotype—but not too extended. A reply to Laland, Turner and Jablonka. *Biology and Philosophy*, 19(3), 377–396. https://doi.org/10.1023/B:BIPH.0000036180.14904.96

de las Casas, B. (2007). *Brevisima relación de la destrucción de las Indias* [A brief account of the destruction of the Indies]. Project Gutenberg EBook No. 20321. http://www.gutenberg.org/ebooks/20321 (Originally work published 1552)

Del Popolo, F., Garcia de Pinto da Cunha, E., Ribotta, B., & Azevedo, M. (Eds.) (2011). Pueblos indígenas y afrodescendientes en América Latina: dinámicas poblacionales diversas y desafíos comunes [Indigenous and Afro-descendant peoples in Latin America: Diverse population dynamics and common challenges]. Serie Investigaciones No. 12. ALAP. https://repositorio.cepal.org/handle/11362/35946

de Saint-Hilaire, A. (1961). Voyage a Rio Grande do Sul (1820–1821). *Anales Históricos de Montevideo*, 4, 307–532.

Deng, L., Ruiz-Linares, A., Xu, S., & Wang, S. (2016). Ancestry variation and footprints of natural selection along the genome in Latin American populations. *Scientific Reports*, 6, 21766. https://doi.org/10.1038/srep21766

Diamond, J. M. (1999). *Guns, germs, and steel: The fates of human societies*. W. W. Norton & Co.

Díaz-Guerrero, R. (2014). *Psychology of the Mexican: Culture and personality*. University of Texas Press.

Domínguez-Bello, M. G., Pérez, M. E., Bortolini, M. C., Salzano, F. M., Pericchi, L. R., Zambrano-Guzman, O., & Linz, B. (2008). Amerindian *Helicobacter pylori* strains go extinct, as European strains expand their host range. *PLOS ONE*, 3(10), e3307. https://doi.org/10.1371/journal.pone.0003307

Dorr, L. L. (2004). *White women, rape, and the power of race in Virginia, 1900–1960*. University of North Carolina Press. http://doi.org/10.1353/sex.2006.0042

Dulik, M. C., Osipova, L. P., & Schurr, T. G. (2011). Y-chromosome variation in Altaian Kazakhs reveals a common paternal gene pool for Kazakhs and the influence of Mongolian expansions. *PLOS ONE*, 6(3), e17548. https://doi.org/10.1371/journal.pone.0017548.t001

Duncan, D. E. (1997). *Hernando de Soto: A savage quest in the Americas*. University of Oklahoma Press. https://doi.org/10.2307/2568462

Dutton, E., & Madison, G. (2017). Why do Finnish men marry Thai women but Finnish women marry British men? Cross-national marriages in a modern, industrialized society exhibit sex-dimorphic sexual selection according to primordial selection pressures. *Evolutionary Psychological Science*, 3(1), 1–9. https://doi.org/10.1007/s40806-016-0068-2

Ebenesersdóttir, S. S., Sigurðsson, A., Sánchez-Quinto, F., Lalueza-Fox, C., Stefánsson, K., & Helgason, A. (2011). A new subclade of mtDNA haplogroup C1 found in Icelanders: Evidence of pre-Columbian contact? *American Journal of Physical Anthropology* 144(1), 92–99. https://doi.org/10.1002/ajpa.21419

Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Mechanisms of environmental risk: The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. *Human Nature*, 20, 204–268. https://doi.org/10.1007/s12110-009-9063-7

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215–223. https://doi.org/10.1126/science.327542

FamilyTree DNA. (2016). *Cuba: Background*. https://www.familytreedna.com/groups/cuba-dna-project/about/background

Fausto, B. (1999). Fazer a América: A imigração em massa para a América *Latina [Making America: Mass immigration to Latin America*]. Editora da Universidade de São Paulo.

Feinman, S., & Gill, G. W. (1978). Sex differences in physical attractiveness preferences. *Journal of Social Psychology*, 105 (1), 43–52. https://doi.org/10.1080/00224545.1978.9924089

Fernald, L. C., & Adler, N. E. (2008). Blood pressure and socioeconomic status in low-income women in Mexico: A reverse gradient? *Journal of Epidemiology and Community Health*, 62(5),e8. https://doi.org/10.1136/jech.2007.065219

Fernández, E., Pérez-Pérez, A., Gamba, C., Prats, E., Cuesta, P., Anfruns, J., Molist, M., Arroyo-Pardo. E., & Turbón, D. (2014). Ancient DNA analysis of 8000 BC near eastern farmers supports an early Neolithic pioneer maritime colonization of mainland Europe through Cyprus and the Aegean Islands. *PLOS Genetics*, 10(6), e1004401. https://doi.org/10.1371/journal.pgen.1004401

Figueredo, A. J., & Wolf, P. S. A. (2009). Assortative pairing and life history strategy: A cross-cultural study. *Human Nature*, 20, 317–330. https://doi.org/10.1007/s12110-009-9068-2

Fitzpatrick, B. M., & Shaffer, H. B. (2007). Introduction history and habitat variation explain the landscape genetics of

hybrid tiger salamanders. *Ecological Applications*, 17(2), 598–608. https://doi.org/10.1890/06-0369

Fitzpatrick, B. M., Johnson, J. R., Kump, D. K., Smith, J. J., Voss, S. R., & Shaffer, H. B. (2010). Rapid spread of invasive genes into a threatened native species. *Proceedings of the National Academy of Sciences*, 107(8), 3606–3610. https://doi.org/10.1073/pnas.0911802107

Florez, J. C., Price, A. L., Campbell, D., Riba, L., Parra, M. V., Yu, F., Duque, C., Saxena, R., Gallego, N., Tello-Ruiz, M., Franco, L., Rodríguez-Torres, M., Villegas, A., Bedoya, G., Aguilar-Salinas, C.A., Tusié-Luna, M. T., Ruiz-Linares, A., & Reich, D. (2009). Strong association of socioeconomic status and genetic ancestry in Latinos: Implications for admixture studies of type 2 diabetes. *Diabetologia*, 52, 1528–1536. https://doi.org/10.1007/s00125-009-1412-x

Francalacci, P., Morelli, L., Useli, A., & Sanna, D. (2010). The history and geography of the Y chromosome SNPs in Europe: An update. *Journal of Anthropological Sciences*, 88, 207–214.

Frisancho, A. R., Wainwright, R., & Way, A. (1981). Heritability and components of phenotypic expression in skin reflectance of Mestizos from the Peruvian lowlands. *American Journal of Physical Anthropology*, 55(2), 203–208. https://doi.org/10.1002/ajpa.1330550207

Gagné, P. (2000). *King's daughters and founding mothers: The filles du roi, 1663–1673* (Vol. 1). Quintin Publications.

García-Deister, V., & López-Beltrán, C. (2015). País de gordos/país de muertos: Obesity, death and nation in biomedical and forensic genetics in Mexico. *Social Studies of Science*, 45(6), 797–815. https://doi.org/10.1177%2F0306312715608449

Garza-Chapa, R. (1983). Genetic distances for ABO and RH(D) blood-groups in the state of Nuevo-León, Mexico. *Social Biology*, 30(1), 24–31. https://doi.org/10.1080/19485565.1983.9988513

Gerber, A. S., Tibbets, C. A., & Dowling, T. E. (2001). The role of introgressive hybridization in the evolution of the Gila robusta complex (Teleostei: Cyprinidae). *Evolution*, 55(10), 2028–2039. https://doi.org/10.1111/j.0014-3820.2001.tb01319.x

Gignoux, C. R., Henn, B. M., & Mountain, J. L. (2011). Rapid, global demographic expansions after the origins of agriculture. *Proceedings of the National Academy of Sciences*, 108(15), 6044–6049. https://doi.org/10.1073/pnas.0914274108

Gonzáles, G. F. (2007). Peruvian contributions to the study on human reproduction at high altitude: From the chronicles of the Spanish conquest to the present. *Respiratory Physiology & Neurobiology*, 158(2), 172–179. https://doi.org/10.1016/j.resp.2007.03.015

González-Martín, A., Gorostiza, A., Rangel-Villalobos, H., Acunha, V., Barrot, C., Sánchez, C., Ortega, M., Gené, M., & Calderón, R. (2008). Analyzing the genetic structure of the Tepehua in relation to other neighbouring Mesoamerican populations: A study based on allele frequencies of STR markers. *American Journal of Human Biology*, 20(5), 605–613. https://doi.org/10.1002/ajhb.20787

Green, L. D., Derr, J. N., & Knight, A. (2000). mtDNA affinities of the peoples of north-central Mexico. *American Journal of Human Genetics*, 66(3), 989–998. https://doi.org/10.1086/302801

Guernier, V., Hochberg, M. E., & Guegan, J. F. (2004). Ecology drives the worldwide distribution of human infectious diseases. *PLOS Biology*, 2(6), e186. https://doi.org/10.1371/journal.pbio.0020186

Guggenheim, C.B., Davis, M.F., & Figueredo, A.J. (2007). Sons or daughters: A cross-cultural study of sex-ratio biasing and differential parental investment. *Journal of the Arizona Nevada Academy of Science*, 39(2), 73–90.

Gutiérrez, R. A. (1985). Honor ideology, marriage negotiation, and class-gender domination in New Mexico, 1690–1846. *Latin American Perspectives*, 12(1), 81–104. https://doi.org/10.1177%2F0094582X8501200105

Hamilton, W. D. (1963). The genetical evolution of social behavior: I and II. *Journal of Theoretical Biology*, 7(1), 1–52. https://doi.org/10.1016/0022-5193(64)90039-6

Hamilton, J. A., & Miller, J. M. (2016). Adaptive introgression as a resource for management and genetic conservation in a changing climate. *Conservation Biology*, 30(1), 33–41. https://doi.org/10.1111/cobi.12574

Harris, M. (1968). *The rise of anthropological theory*. HarperCollins.

Hartung, J. (1982). Polygyny and inheritance of wealth. *Current Anthropology*, 23(1), 1–12.

Hatfield, E., & Sprecher, S. (1995). Men's and women's preferences in marital partners in the United States, Russia, and Japan. *Journal of Cross-Cultural Psychology*, 26(6), 728–750. https://doi.org/10.1177%2F002202219502600613

Hecht, T. (2002). *Minor omissions: Children in Latin American history and society*. University of Wisconsin Press.

Hedrick, P. W. (2013). Adaptive introgression in animals: Examples and comparison to new mutation and standing variation as sources of adaptive variation. *Molecular Ecology*, 22(18), 4606–4618. https://doi.org/10.1111/mec.12415

Hertler, S., Figueredo, A. J., & Peñaherrera Aguirre, M. (2020). *Multi-level selection: Theoretical foundations, historical examples, and empirical evidence*. Palgrave Macmillan.

Homburger, J. R., Moreno-Estrada, A., Gignoux, C. R, Nelson, D., Sanchez, E., Ortiz-Tello, P., Pons-Estel, B. A., Acevedo-Vasquez, E., Miranda, P., Langefeld, C. D., Gravel, S., Alarcón-Riquelme, M. E., & Bustamante, C. D. (2015). Genomic insights into the ancestry and demographic history of

South America. *PLOS Genetics*, 11(12), e1005602. https://doi.org/10.1371/journal.pgen.1005602

Hopenhayn, M., Bello, A., & Miranda, F. (2006). Los pueblos indígenas y afrodescendientes ante el nuevo milenio [Indigenous and Afro-descendant peoples facing the new millennium]. Serie Políticas Sociales No. 118. CEPAL. https://repositorio.cepal.org/handle/11362/6123

Hourani, A. (2013). *A history of the Arab peoples* (Updated ed.). Faber & Faber.

Huerta-Sanchez, E., & Casey, F. P. (2015). Archaic inheritance: supporting high-altitude life in Tibet. *Journal of Applied Physiology*, 119(10), 1129–1134. https://doi.org/10.1152/japplphysiol.00322.2015

Huerta-Sanchez, E., Jin, X, Asan, Bianba, Z., Peter, B. M., Vinckenbosch, N., Liang, Y., Yi, X., He, M., Somel, M., Ni, P., Wang, B., Ou, X., Huasang, Luosang, J., Cuo, Z. X. P., Li, K., Gao, G., Yin, Y., . . . Nielsen, R. (2014). Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature*, 512(7513), 194–197. https://doi.org/10.1038/nature13408

Hughes, A. R., Inouye, B. D., Johnson, M. T., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, 11(6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

Ingoldsby, B. B. (1991). The Latin American family: Familism vs. machismo. *Journal of Comparative Family Studies*, 22(1), 57–62.

Isola, E. (1975). *La esclavitud en el Uruguay desde sus comienzos hasta su extinción (1743–1852)* [Slavery in Uruguay from its beginnings to its extinction (1743–1852)]. Comisión Nacional de Homenaje del Sesquicentenario de los Hechos Históricos de 1825. Talleres Gráficos Monteverde y Cía.

Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT Press. https://doi.org/10.1172%2FJCI27017

Jha, S., & Adelman, M. (2009). Looking for love in all the white places: A study of skin color preferences on Indian matrimonial and mate-seeking websites. *Studies in South Asian Film & Media*, 1(1), 65–83. https://doi.org/10.1386/safm.1.1.65_1

Jobling, M., Hollox, E., Hurles, M., Kivisild, T., & Tyler-Smith, C. (2013). *Human evolutionary genetics*. Garland Science. https://doi.org/10.1201/9781317952268

Jordan, I. K. (2016). The Columbian Exchange as a source of adaptive introgression in human populations. *Biology Direct*, 11(1), 17. https://doi.org/10.1186/s13062-016-0121-x

Kanazawa, S. (2005). Big and tall parents have more sons: Further generalizations of the Trivers-Willard hypothesis.

Journal of Theoretical Biology, 235(4), 583–590. https://doi.org/10.1016/j.jtbi.2005.02.010

Katoh, T., Munkhbat, B., Tounai, K., Mano S., Ando H., Oyungerel G., Chae, G. T., Han, H., Jia, G. J., Tokunaga, K., Munkhtuvshin, N., Tamiya, G., & Inoko, H. (2005). Genetic features of Mongolian ethnic groups revealed by Y-chromosomal analysis. *Gene*, 346, 63–70. https://doi.org/10.1016/j.gene.2004.10.023

Keller, M. C., Nesse, R. M., & Hofferth, S. (2001). The Trivers-Willard hypothesis of parental investment: No effect in the contemporary United States. *Evolution and Human Behavior*, 22(5), 343–360. https://doi.org/10.1016/S1090-5138(01)00075-7

Keller, S. R., & Taylor, D. R. (2010). Genomic admixture increases fitness during a biological invasion. *Journal of Evolutionary Biology*, 23(8), 1720–1731. https://doi.org/10.1111/j.1420-9101.2010.02037.x

Kidd, J.M., Gravel, S., Byrnes, J., Moreno-Estrada, A., Musharoff, S., Bryc, K., Degenhardt, J. D., Brisbin, A., Sheth, V., Chen, R., McLaughlin, S. F., Peckham, H. E., Omberg, L., Bormann Chung, C. A., Stanley, S., Pearlstein, K., Levandowsky, E., Acevedo-Acevedo, S., Auton, A., . . . Bustamante, C. D. (2012). Population genetic inference from personal genome data: Impact of ancestry and admixture on human genomic variation. *American Journal of Human Genetics*, 91(4), 660–671. https://doi.org/10.1016/j.ajhg.2012.08.025

Kirkwood, B. (2000). *History of Mexico*. Greenwood Press.

Kvarnemo, C., & Ahnesjö, I. (1996). The dynamics of operational sex rations and competition for mates. *Trends in Ecology and Evolution*, 11(10), 404–408. https://doi.org/10.1016/0169-5347(96)10056-2

Lacan, M., Keyser, C., Ricaut, F.X., Brucato, N., Tarrús, J., Bosch, A., Guilaine, J., Crubézy, E., & Ludes, B. (2011). Ancient DNA suggests the leading role played by men in the Neolithic dissemination. *Proceedings of the National Academy of Sciences*, 108(45), 18255–18259. https://doi.org/10.1073/pnas.1113061108

Laland, K. N., & O'Brien, M. J. (2011). Cultural niche construction: An introduction. *Biological Theory*, 6(3), 191–202. https://doi.org/10.1007/s13752-012-0026-6

Langness, L. L. (1974). *The study of culture* (Revised ed.). Chandler & Sharp.

Leite, F. P. N., Callegari-Jacques, S. M., Carvalho, B. A., Kommers, T., Matte, C. H. F., & Raimann, P. E., *et al.* (2008). Y-STR Analysis in Brazilian and South Amerindian populations. *American Journal of Human Biology*, 20(3), 359–363. https://doi.org/10.1002/ajhb.20702

Li, S., Schlebusch, C., & Jakobsson, M. (2014). Genetic variation reveals large-scale population expansion and migration during the expansion of Bantu-speaking peoples.

Proceedings of the Royal Society of London B, 281(1793), 20141448. https://doi.org/10.1098/rspb.2014.1448

Lind, J. M., Hutcheson-Dilks, H. B., Williams, S. M., Moore, J. H., Essex, M., Ruiz-Pesini, E., Wallace, D. C., Tishkoff, S. A., O'Brien, S. J., & Smith, M. W. (2007). Elevated male European and female African contributions to the genomes of African American individuals. *Human genetics*, 120(5), 713–722. https://doi.org/10.1007/s00439-006-0261-7

Lisker, R., Ramírez, E., Gonzalez-Villalpando, C., & Stern, M. P. (1995). Racial admixture in a Mestizo population from Mexico City. *American Journal of Human Biology*, 7(2), 213–216. https://doi.org/10.1002/ajhb.1310070210

Lumsden, C. J., & Wilson, E. O. (1981). *Genes, mind, and culture*. Harvard University Press. https://doi.org/10.1017/S002193200001453X

Lynn, R. (2008). Pigmentocracy: Racial hierarchies in the Caribbean and Latin America. *Occidental Quarterly*, 8(2), 25–44.

Marmot, M. G., Smith, G. D., Stansfeld, S., Patel, C., North, F., Head, J., White, I., Brunner, E., & Feeney, A. (1991). Health inequalities among British civil servants: The Whitehall II study. *The Lancet*, 337(8754), 1387–1393. https://doi.org/10.1016/0140-6736(91)93068-k

Martin, D. L., & Goodman, A. H. (2002). Health conditions before Columbus: Paleopathology of native North Americans. *Western Journal of Medicine*, 176(1), 65–68. https://doi.org/10.1136/ewjm.176.1.65

Martínez Marignac, V. L., Bertoni, B., Parra, E. J., & Bianchi, N. O. (2004). Characterization of admixture in an urban sample from Buenos Aires, Argentina, using uniparentally and biparentally inherited genetic markers. *Human Biology*, 76(4), 543–557. https://doi.org/10.1353/hub.2004.0058

Martinsen, G. D., Whitham, T. G., Turek, R. J., & Keim, P. (2001). Hybrid populations selectively filter gene introgression between species. *Evolution*, 55(7), 1325–1335. https://doi.org/10.1111/j.0014-3820.2001.tb00655.x

McBride-Limaye, A. (1988). Metamorphoses of La Malinche and Mexican cultural identity. *Comparative Civilization Review*, 19, 1–27.

McGuire, D. L. (2011). *At the dark end of the street: Black women, rape, and resistance—A new history of the civil rights movement from Rosa Parks to the rise of Black Power*. Vintage.

Moreno-Estrada, A., Gignoux, C. R., Fernández-López, J. C., Zakharia, F., Sikora, M., Contreras, A. V., Acuña-Alonzo, V., Sandoval, K., Eng, C., Romero-Hidalgo, S., Ortiz-Tello, P., Robles, V., Kenny, E. E., Nuño-Arana, I., Barquera-Lozano, R., Macín-Pérez, G., Granados-Arriola, J., Huntsman, S., Galanter, J. M., Via, M., . . . Bustamante, C. D. (2014). The genetics of Mexico recapitulates Native American substructure and affects biomedical traits. *Science*, 344(6189), 1280–1285. https://doi.org/10.1126/science.1251688

Moreno Figueroa, M. G. (2010). Distributed intensities: Whiteness, mestizaje and the logics of Mexican racism. *Ethnicities*, 10(3), 387–401. https://doi.org/10.1177%2F1468796810372305

Morera, B., Barrantes, R., & Marin-Rojas, R. (2003). Gene admixture in the Costa Rican population. *Annals of Human Genetics*, 67(1), 71–80. https://doi.org/10.1046/j.1469-1809.2003.00010.x

Morgan, L. H. (1877). *Ancient society, or researches in the lines of human progress, from savagery through barbarism to civilization*. Henry Holt & Co. http://www.gutenberg.org/files/45950/45950-h/45950-h.htm

Mulligan, C. J., Hunley, K., Cole, S., & Long, J. C. (2004). Population genetics, history, and health patterns in Native Americans. *Annual Review of Genomics and Human Genetics*, 5, 295–315. https://doi.org/10.1146/annurev.genom.5.061903.175920

Nabhan, G. P. (2012). *Desert terroir: Exploring the unique flavors and sundry places of the Borderland*. University of Texas Press.

Nebel, A., Filon, D., Brinkmann, B., Majumder, P. P., Faerman, M., & Oppenheim, A. (2001). The Y chromosome pool of Jews as part of the genetic landscape of the Middle East. *American Journal of Human Genetics*, 69(5), 1095–1112. https://doi.org/10.1086/324070

Negrotto, L., & Correale, J. (2018). Evolution of multiple sclerosis prevalence and phenotype in Latin America. *Multiple Sclerosis and Related Disorders*, 22, 97–102. https://doi.org/10.1016/j.msard.2018.03.014

Norris, L. C., Main, B. J., Lee, Y., Collier, T. C., Fofana, A., Cornel, A. J., & Lanzaro, G. C. (2015). Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets. *Proceedings of the National Academy of Sciences*, 112(3), 815–820. https://doi.org/10.1073/pnas.1418892112

Nothnagel, M., Fan, G., Guo, F., He, Y., Hou, Y., Hu, S., Huang, J., Jiang, X., Kim, W., Kim, K., Li, C., Li, H., Li, L., Li, S., Li, Z., Liang, W., Liu, C., Lu, D., Luo, H., . . . , Roewer, L. (2017). Revisiting the male genetic landscape of China: A multi-center study of almost 38,000 Y-STR haplotypes. *Human Genetics*, 136, 485–497. https://doi.org/10.1007/s00439-017-1759-x

Núñez Seixas, X. M. (Ed.) (2001). La Galicia Austral: La inmigración gallega en la Argentina *[Austral Galicia: Galician immigration in Argentina]*. Biblos.

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton University Press.

Okasha, S. (2006). *Evolution and levels of selection*. Oxford University Press.

Oldstone, M. (2009). *Viruses, plagues, and history: Past, present and future*. Oxford University Press.

Ongaro, L., Scliar, M. O., Flores, R., Raveane, A., Marnetto, D., Sarno, S., Gnecchi-Ruscone, G. A., Alarcon-Riquelme, M., Patin, E., Wangkumhang, P., Hellenthal, G., Gonzalez-Santos, M., King, R. J., Kouvatsi, A., Balanovsky, O., Balanovska, E., Atramentova, L., Turdikulova, S., Mastana, S., . . . Montinaro, F. (2019). The genomic impact of European colonization of the Americas. *bioRxiv*, 676437. https://doi.org/10.1101/676437

Organización Panamericana de la Salud (OPS). (2012). *Salud de las Américas: Panorama regional y perfiles de país*. [Health of the Americas: Regional panorama and country profiles]. https://www.paho.org/salud-en-las-americas-2012/index.php?option=com_content&view=article&id=9:edicion-2012&Itemid=124&lang=es

Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist*, 103(934), 589–603.

Pardo-Díaz, C., Salazar, C., Baxter, S. W., Merot, C., Figueiredo-Ready, W., Joron, M., McMillan, W. O., & Jiggins, C. D. (2012). Adaptive introgression across species boundaries in Heliconius butterflies. *PLOS Genetics*, 8(6), e1002752. https://doi.org/10.1371/journal.pgen.1002752

Perreira, K. M & Telles, E. E. (2014). The color of health: Skin color, ethnoracial classification, and discrimination in the health of Latin Americans. *Social Science & Medicine*, 116, 241–250. https://doi.org/10.1016/j.socscimed.2014.05.054

Pimentel, H. (2005). O casamento no Brasil Colonial: Um ensaio historiográfico [Marriage in colonial Brazil: A historiographical essay]. *Em Tempo de Histórias*, 9, 20–38.

Pribil, S., & Searcy, W. A. (2001). Experimental confirmation of the polygyny threshold model for red-winged blackbirds. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 1643–1646. https://doi.org/10.1098/rspb.2001.1720

Ptak, S. E. & Lachmann, M. (2003). On the evolution of polygyny: A theoretical examination of the polygyny threshold model. *Behavioral Ecology*, 14(2), 201–211. https://doi.org/10.1093/beheco/14.2.201

Quijano, A. (2000). Coloniality of power and eurocentrism in Latin America. *International Sociology* 15(2), 215–232. https://doi.org/10.1177%2F0268580900015002005

Racimo, F., Marnetto, D., & Huerta-Sánchez, E. (2016). Signatures of archaic adaptive introgression in present-day human populations. *Molecular Biology and Evolution*, 34(2), 296–317. https://doi.org/10.1093/molbev/msw216

Rangel-Villalobos, H., Rivas, F., Sandoval, L., Ibarra, B., Garcia-Carvajal, Z. Y., Cantu, J. M., & Figuera, L. E. (2000).

Genetic variation among four Mexican populations (Huichol, Purepecha, Tarahumara, and Mestizo) revealed by two VNTRs and four STRs. *Human Biology*, 72(6), 983–995.

Regueiro, M., Garcia-Bertrand, R., Fadhlaoui-Zid, K., Álvarez, J., & Herrera, R. J. (2015). From Arabia to Iberia: A Y chromosome perspective. *Gene*, 564(2), 141–152. https://doi.org/10.1016/j.gene.2015.02.042

Reich, D., Thangaraj, K., Patterson, N., Price, A. L., & Singh, L. (2009). Reconstructing Indian population history. *Nature*, 461(7263), 489–494. https://doi.org/10.1038/nature08365

Rendell, L., Fogarty, L., & Laland, K. N. (2011). Runaway cultural niche construction. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1566), 823–835. https://doi.org/10.1098/rstb.2010.0256

Richards, E. J., & Martin, C. H. (2017). Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic radiation of trophic specialist pupfishes. *bioRxiv*, 115055. https://doi.org/10.1371/journal.pgen.1006919

Richards, M., Macaulay, V., Hickey, E., Vega, E., Sykes, B., Guida, V., Rengo, C., Sellitto, D., Cruciani, F., Kivisild, T., Villems, R., Thomas, M., Rychkov, S., Rychkov, O., Rychkov, Y., Gölge, M., Dimitrov, D., Hill, E., Bradley, D., . . . Bandelt, H. J. (2000). Tracing European founder lineages in the Near Eastern mtDNA pool. *American Journal of Human Genetics*, 67(5), 1251–1276.

Richards, M., Rengo, C., Cruciani, F., Gratrix, F., Wilson, J. F., Scozzari, R., . . . & Torroni, A. (2003). Extensive female-mediated gene flow from sub-Saharan Africa into near eastern Arab populations. *American Journal of Human Genetics*, 72(4), 1058–1064. https://doi.org/10.1086/374384

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How cultural transformed human evolution*. University of Chicago Press.

Rieseberg, L. (2011). Adaptive introgression: The seeds of resistance. *Current Biology*, 21(15), R581–R583. https://doi.org/10.1016/j.cub.2011.06.038

Risch, N., Choudhry. S., Via, M., Basu, A., Sebro, R., Eng, C., Beckman, K., Thyne, S., Chapela, R., Rodriguez-Santana, J. R., Rodriguez-Cintron, W., Avila, P. C., Ziv, E., & Gonzalez Burchard, E. (2009). Ancestry-related assortative mating in Latino populations. *Genome Biology*, 10, 132. https://doi.org/10.1186/gb-2009-10-11-r132

Ritterman, M. L., Fernald, L. C., Ozer, E. J., Adler, N. E., Gutierrez, J. P., & Syme, S. L. (2009). Objective and subjective social class gradients for substance use among Mexican adolescents. *Social Science & Medicine*, 68, 1843–1851. https://doi.org/10.1016/j.socscimed.2009.02.048

Rocco, P., Morales, C., Moraga, M., Miquel, J. F., Nervi, F., Llop, E., Carvallo, P., & Rothhammer, F. (2002). Composición

genética de la población chilena: Distribución de polimorfismos de DNA mitocondrial en grupos originarios y en la población mixta de Santiago [Genetic composition of the Chilean population: Distribution of mitochondrial DNA polymorphisms among native groups and mixed population of Santiago]. *Revista Médica de Chile*, 130(2), 125–131. https://doi.org/10.4067/S0034-98872002000200001

Rodríguez, E. (2008). *The Costa Rican families during the eighteenth, nineteenth and twentieth centuries*. Editorial UCR.

Rojas, W., Parra, M. V., Campo, O., Caro, M. A., Lopera, J. G., Arias, W., Duque, C., Naranjo, A., García, J., Vergara, C., Lopera, J., Hernandez, E., Valencia, A., Caicedo, Y., Cuartas, M., Gutiérrez, J., López, S., Ruiz-Linares, A., & Bedoya, G. (2010). Genetic make up and structure of Colombian populations by means of uniparental and biparental DNA markers. *American Journal of Physical Anthropology*, 143(1), 13–20. https://doi.org/10.1002/ajpa.21270

Rotimi, C. N., Tekola-Ayele, F., Baker, J. L., & Shriner, D. (2016). The African diaspora: History, adaptation and health. *Current Opinion in Genetics & Development*, 41, 77–84. https://doi.org/10.1016%2Fj.gde.2016.08.005

Rowley-Conwy, P., & Layton, R. (2011). Foraging and farming as niche construction: Stable and unstable adaptations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366(1566), 849–862. https://doi.org/10.1098%2Frstb.2010.0307

Rowold, D., Garcia-Bertrand, R., Calderon, S., Rivera, L., Benedico, D. P., Alfonso Sanchez, M. A., Chennakrishnaiah, S., Varela, M., Herrera, R. J. (2014). At the southeast fringe of the Bantu expansion: Genetic diversity and phylogenetic relationships to other sub-Saharan tribes. *Meta Gene*, 2, 670–685. https://doi.org/10.1016/j.mgene.2014.08.003

Rushton, J. P. (1989). Genetic similarity, human altruism, and group selection. *Behavioral and Brain Sciences*, 12(3), 503–559. https://doi.org/10.1017/S0140525X00057320

Ryabov, I. (2016). Educational outcomes of Asian and Hispanic Americans: The significance of skin color. *Research in Social Stratification and Mobility*, 44, 1–9. http://doi.org/10.1016/j.rssm.2015.11.001

Saint-Paul, G. (2015). Genes, legitimacy, and hypergamy: Another look at the economics of marriage. *Journal of Demographic Economics*, 81(4), 331–337. https://doi.org/10.1017/dem.2015.8

Salas, A., Richards, M., Lareu, M. V., Scozzari, R., Coppa, A., Torroni, A., Macaulay, V., & Carracedo, A. (2004). The African diaspora: Mitochondrial DNA and the Atlantic slave trade. *American Journal of Human Genetics*, 74(3), 454–465. https://doi.org/10.1086/382194

Salzano, F. M. (2004). Interethnic variability and admixture in Latin America: Social implications. *Revista de Biología Tropical*, 52(3), 405–415. https://doi.org/10.15517/rbt.v1i2.15273

Salzano, F. M., & Bortolini, M. C. (2002). *The evolution and genetics of Latin American populations*. Cambridge University Press. https://doi.org/10.1093/jhered/93.5.387

Sanchez, M. E. (1998). La Malinche at the intersection: Race and gender down these mean streets. *PMLA*, 113(1), 117–118. https://doi.org/10.2307/463413

Sans, M. (2000). Admixture studies in Latin America: From the 20th to the 21st century. *Human Biology*, 72(1), 155–177.

Sans, M., Weimer, T. A., Franco, M. H. L., Salzano, F. M., Bentancor, N., Alvarez, I., Bianchi, N. O., & Chakraborty, R. (2002). Unequal contributions of male and female gene pools from parental populations in the African descendants of the city of Melo, Uruguay. *American Journal of Physical Anthropology*, 118(1), 33–44. https://doi.org/10.1002/ajpa.10071

Santiago-Torres, M., Kratz, M., Lampe, J. W., Tapsoba, J. de D., Breymeyer, K. L., Levy, L., Villaseñor, A., Wang, C. Y., Song, X., & Neuhouser, M. L. (2017). Genetic ancestry in relation to the metabolic response to a US versus traditional Mexican diet: A randomized crossover feeding trial among women of Mexican descent. *European Journal of Clinical Nutrition*, 71(3), 395–401. https://doi.org/10.1038/ejcn.2016.211

Semino, O., Passarino, G., Oefner, P. J., Lin, A. A., Arbuzova, S., Beckman, L. E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., Marcikiæ, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A., S., Cavalli-Sforza, L. L., & Underhill, P. A. (2000). The genetic legacy of Paleolithic *Homo sapiens sapiens* in extant Europeans: AY chromosome perspective. *Science*, 290(5494), 1155–1159. https://doi.org/10.1126/science.290.5494.1155

Silva, M., Oliveira, M., Vieira, D., Brandão, A., Rito, T., Pereira, J. B., Fraser, R. M., Hudson, B., Gandini, F., Edwards, C., Pala, M., Koch, J., Wilson, J. F., Pereira, L., Richards, M. B., & Soares, P. (2017). A genetic chronology for the Indian subcontinent points to heavily sex-biased dispersals. *BMC Evolutionary Biology*, 17(1), 88. http://doi.org/10.1186/s12862-017-0936-9

Silva-Zolezzi, I., Hidalgo-Miranda, A., Estrada-Gil, J., Fernandez-Lopez, J. C., Uribe-Figueroa, L., Contreras, A., Balam-Ortiz, E., del Bosque-Plata, L., Velazquez-Fernandez, D., Lara C., Goya, R., Hernandez-Lemus, E., Davila, C., Barrientos, E., March, S., & Jimenez-Sanchez, G. (2009). Analysis of genomic diversity in Mexican mestizo populations to develop genomic medicine in Mexico. *Proceedings of the National Academy of Sciences*, 106(21), 8611–8616. https://doi.org/10.1073/pnas.0903045106

Sjödin, P., & François, O. (2011). Wave-of-advance models of the diffusion of the Y chromosome haplogroup R1b1b2 in Europe. *PLOS ONE*, 6(6), e21592. https://doi.org/10.1371/journal.pone.0021592

Skidmore, T. E., & Smith, P. H. (2005). *Modern Latin America* (6th ed.). Oxford University Press.

Smith, C. A. (1997). The symbolics of blood: Mestizaje in the Americas. *Identities*, 3(4), 495–521. https://doi.org/10.1080/1070289X.1997.9962576

Smith-Castro, V. (2005). Discriminación percibida y autoestima en jóvenes de grupos minoritarios y mayoritarios en Costa Rica [Perceived discrimination and self/esteem among youths from minority and majority groups in Costa Rica]. *Revista Interamericana de Psicología*, 39, 93–106.

Smith-Castro, V. (2010). Experiencias de discriminación social de inmigrantes nicaragüenses en Costa Rica: Reacciones afectivas y atribuciones causales [Experiences of social discrimination among Nicaraguan immigrants in Costa Rica: Affective reactions and causal attributions]. *Revista Interamericana de Psicología*, 42, 368–381.

Smuts, B. (2007). *Sex and friendship in baboons*. Aldine Transaction.

Song, Y., Endepols, S., Klemann, N., Richter, D., Matuschka, F. R., Shih, C. H., Nachman, M. W., & Kohn, M. H. (2011). Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice. *Current Biology*, 21(15), 1296–1301. https://doi.org/10.1016/j.cub.2011.06.043

Sotomayor-Peterson, M., Cabeza de Baca, T., Figueredo, A.J., & Smith-Castro, V. (2013). Shared parenting, parental effort, and life history strategy: A cross-cultural comparison. *Journal of Cross-Cultural Psychology*, 44(4), 620–639.

Soto Quirós, R. (2009). Imaginando una nación de raza blanca en Costa Rica: 1821–1914. [Imaging a White nation in Costa Rica: 1821–1914]. *Amérique Latine Histoire et Mémoire*, 15. http://journals.openedition.org/alhim/2930

Stevens, E. P. (1973). Machismo and marianismo. *Society*, 10, 57–63. https://doi.org/10.1007/BF02695282

Stoddard, P., Handley, M. A., Bustamante, A. V., & Schillinger, D. (2011). The influence of indigenous status and community indigenous composition on obesity and diabetes among Mexican adults. *Social Science & Medicine*, 73, 1635–1643. https://doi.org/10.1016/j.socscimed.2011.09.006

Symons, D. (1995). Beauty is in the adaptations of the beholder: The evolutionary psychology of human female sexual attractiveness. In P. R. Abramson & S. D. Pinkerton (Eds.), *Sexual nature/sexual culture* (pp. 80–118). University of Chicago Press.

Tang, H., Choudhry, S., Mei, R., Morgan, M., Rodriguez-Cintron, W., Burchard, E. G., & Risch, N. J. (2007). Recent genetic selection in the ancestral admixture of Puerto Ricans. *American Journal of Human Genetics*, 81(3), 626–633. https://doi.org/10.1086%2F520769

Telles, E. E. (2014). Pigmentocracies: Ethnicity, race, and color in Latin America. University of North Carolina Press.

Telles, E., Flores, R. D., & Urrea-Giraldo, F. (2015). Pigmentocracies: Educational inequality, skin color and census ethnoracial identification in eight Latin American countries. *Research in Social Stratification and Mobility*, 40, 39–58. https://doi.org/10.1016/j.rssm.2015.02.002

Telles, E. E., & Sue, C. A. (2009). Race mixture: Boundary crossing in comparative perspective. *Annual Review of Sociology*, 35, 129–146. https://doi.org/10.1146/annurev.soc.34.040507.134657

Terreros, M. C., Rowold, D. J., Mirabal, S., & Herrera, R. J. (2011). Mitochondrial DNA and Y-chromosomal stratification in Iran: Relationship between Iran and the Arabian Peninsula. *Journal of Human Genetics*, 56(3), 235–246. https://doi.org/10.1038/jhg.2010.174

Thomson, M. (1998). Junior division winner: The Migration of smallpox and its indelible footprint on Latin America history. *The History Teacher*, 32(1), 117–131.

Torroni, A., Bandelt, H. J., Macaulay, V., Richards, M., Cruciani, F., Rengo, C., Martinez-Cabrera, V., Villems, R., Kivisild, T., Metspalu, E., Parik, J., Tolk, H. V., Tambets, K., Forster, P., Karger, B., Francalacii, P., Pavao, R., Janicijevic, B., Rickards, O., . . . Scozzari, R. (2001). A signal, from human mtDNA, of postglacial recolonization in Europe. *American Journal of Human Genetics*, 69(4), 844–852. https://doi.org/10.1086%2F323485

Triki-Fendri, S., & Rebai, A. (2014). Synthetic review on the genetic relatedness between North Africa and Arabia deduced from paternal lineage distributions. *International Journal of Modern Anthropology*, 1(7), 100–111. http://doi.org/10.4314/ijma.v1i7.5

Tung, J., Charpentier, M. J., Mukherjee, S., Altmann, J., & Alberts, S. C. (2012). Genetic effects on mating success and partner choice in a social mammal. *American Naturalist*, 180 (1), 113–129. https://doi.org/10.1086/665993

Tuttle, E. M., Bergland, A. O., Korody, M. L., Brewer, M. S., Newhouse, D. J., Minx, P., Stager, M., Betuel, A., Cheviron, Z. A., Warren, W. C., Gonser, R. A., & Balakrishnan, C. N. (2016). Divergence and functional degradation of a sex chromosome-like supergene. *Current Biology*, 26(3), 344–350. https://doi.org/10.1016/j.cub.2015.11.069

Twyford, A. D., & Ennos, R. A. (2012). Next-generation hybridization and introgression. *Heredity*, 108(3), 179–189. https://doi.org/10.1038%2Fhdy.2011.68

United Nations International Children's Emergency Fund (UNICEF). (2009). *Atlas Sociolingüístico de Pueblos Indígenas de America Latina* [Sociolinguistic atlas of indigenous peoples of Latin America]. https://www.unicef.org/tomo_1_atlas.pdf

Vandenberg, S. G. (1972). Assortative mating, or who marries whom? *Behavior Genetics*, 2, 127–157. https://doi.org/10.1007/BF01065686

Vasquez, E. E., & Deister, V. G. (2019). Mexican samples, Latino DNA: The trajectory of a national genome in transnational science. Engaging Science, Technology, and Society, 5, 107–134. https://doi.org/10.17351/ests2019.199

Vijayakumar, P., Wheelock, K. M., Kobes, S., Nelson, R. G., Hanson, R. L., Knowler, W. C., & Sinha, M. (2018). Secular changes in physical growth and obesity among southwestern American Indian children over four decades. *Pediatric Obesity*, 13(2), 94–102. https://doi.org/10.1111/ijpo.12199

Villarreal, A. (2010). Stratification by skin color in contemporary Mexico. *American Sociological Review*, 75(5), 652–678. https://doi.org/10.1177%2F0003122410378232

vonHoldt, B. M., Kays, R., Pollinger, J. P., & Wayne, R. K. (2016). Admixture mapping identifies introgressed genomic regions in North American canids. *Molecular Ecology*, 25(11), 2443–2453. https://doi.org/10.1111/mec.13667

Wade, P. (2008). Race in Latin America. In D. Poole (Ed.), *A Companion to Latin American Anthropology* (pp. 177–192). Oxford University Press.

Wade, P. (2017a). Degrees of mixture, degrees of freedom: Genomics, multiculturalism, and race in Latin America. Duke University Press.

Wade, P. (2017b). *Race and ethnicity in Latin America*. Pluto Press.

Wade, P., Beltrán, C. L., Restrepo, E., & Santos, R. V. (Eds.). (2014). Mestizo genomics: Race mixture, nation, and science in Latin America. Duke University Press.

Waldman, C. (2009). *Atlas of the North American Indian*. Checkmark.

Wang, S., Lewis, C. M., Jakobsson, M., Ramachandran, S., Ray, N., Bedoya, G., Rojas, W., Parra, M. V., Molina, J. A., Gallo, C., Mazzotti, G., Poletti, G., Hill, K., Hurtado, A. M., Labuda, D., Klitz, W., Barrantes, R., Bortolini, M. C., Salzano, F. M., Petzl-Erler, M. L., . . . Ruiz-Linares A. (2007). Genetic variation and population structure in Native Americans. *PLOS Genetics*, 3(11), e185. https://doi.org/10.1371/journal.pgen.0030185

Wang, S., Ray, N., Rojas, W., Parra M. V., Bedoya, G., Gallo, C., Poletti, G., Mazzotti, G., Hill, K., Hurtado, A. M., Camrena, B., Nicolini, H., Klitz, W., Barrantes, R., Molina, J. A., Freimer, N. B., Bortolini, M. C., Salzano, F. M., Petzl-Erler, M. L., . . . Ruiz-Linares, A. (2008). Geographic patterns of genome admixture in American mestizos. *PLOS Genetics*, 4 (3), e1000037. https://doi.org/10.1371/journal.pgen.1000037

Watts, S. (2001). Yellow fever immunities in West Africa and the Americas in the age of slavery and beyond: A reappraisal. *Journal of Social History*, 34(4), 955–967. https://doi.org/10.1353/jsh.2001.0071

Weale, M. E., Weiss, D. A., Jager, R. F., Bradman, N., & Thomas, M. G. (2002). Y chromosome evidence for Anglo-Saxon mass migration. *Molecular Biology and Evolution*, 19(7), 1008–1021. https://doi.org/10.1093/oxfordjournals.molbev.a004160

Wen, B., Li, H., Lu, D., Song, X., Zhang, F., He, Y., Li, F., Gao, Y., Mao, X., Zhang, L., Qian, J., Tan J., Jin, J., Huang, W., Deka, R., Su, B., Chakraborty, R., & Jin, L. (2004). Genetic evidence supports demic diffusion of Han culture. *Nature*, 431(7006), 302–305. https://doi.org/10.1038/nature02878

White, D. R., & Burton, M. L. (1988). Causes of polygyny: Ecology, kinship, and warfare. American Anthropologist, *new series*, 90, 871–887. https://doi.org/10.1525/aa.1988.90.4.02a00060

Williams, D. R., Mohammed, S. A., Leavell, J., & Collins, C. (2010). Race, socioeconomic status, and health: Complexities, ongoing challenges, and research opportunities. *Annals of the New York Academy of Sciences*, 1186, 69–101. https://doi.org/10.1111/j.1749-6632.2009.05339.x

Wood, E. T., Stover, D. A., Ehret, C., Destro-Bisol, G., Spedini, G., McLeod, H., Louie, L., Bamshad, M., Strassmann, B. I., Soodyall, H., & Hammer, M. F. (2005). Contrasting patterns of Y chromosome and mtDNA variation in Africa: Evidence for sex-biased demographic processes. *European Journal of Human Genetics*, 13(7), 867–876. https://doi.org/10.1038/sj.ejhg.5201408

Xu, S., Yin, X., Li, S., Jin, W., Lou, H., Yang, L., Gong, X., Wang, H., Shen, Y., Pan, X., He, Y., Yang, Y., Wang, Y., Fu, W., An, Y., Wang, J., Tan, J., Qian, J., Chen, X., . . . Jin, L. (2009). Genomic dissection of population substructure of Han Chinese and its implication in association studies. *American Journal of Human Genetics*, 85(6), 762–774. https://doi.org/10.1016/j.ajhg.2009.10.015

Yalcindag, E., Elguero, E., Arnathau, C., Durand, P., Akiana, J., Anderson, TJ., Aubouy, A., Balloux, F., Besnard, P., Bogreau, H., Carnevale, P., D'Alessandro, U., Fontenille, D., Gamboa, D., Jombart, T., Le Mire, J., Leroy, E., Maestre, A., Mayxay, M., . . . Prugnolle, F. (2012). Multiple independent introductions of Plasmodium falciparum in South America. *Proceedings of the National Academy of Sciences*, 109(2), 511–516. https://doi.org/10.1073/pnas.1119058109

Yamagishi, T., & Hashimoto, H. (2016). Social niche construction. *Current Opinion in Psychology*, 8, 119–124. https://doi.org/10.1016/j.copsyc.2015.10.003

Zerjal, T., Wells, R. S., Yuldasheva, N., Ruzibakiev, R., & Tyler-Smith, C. (2002). A genetic landscape reshaped by recent events: Y-chromosomal insights into central Asia. *American Journal of Human Genetics*, 71(3), 466–482. https://doi.org/10.1086/342096

Zerjal, T., Xue, Y., Bertorelle, G., Wells, R. S., Bao, W., Zhu, S., Qamar, R., Ayub, Q., Mohyuddin, A., Fu, S., Li, P., Yuldasheva, N., Ruzibakiev, R., Xu, J., Shu, Q., Du, R., Yang, H., Hurles, M. E., Robinson, E., . . . Tyler-Smith, C. (2003). The genetic legacy of the Mongols. *American Journal of Human Genetics*, 72(3), 717–721. https://doi.org/10.1086/367774

Zhao, Z., Khan, F., Borkar, M., Herrera, R., & Agrawal, S. (2009). Presence of three different paternal lineages among North Indians: A study of 560 Y chromosomes. *Annals of Human Biology*, 36(1), 46–59. https://doi.org/10.1080/03014460802558522

Zhou, Q., Zhao, L., & Guan, Y. (2016). Strong selection at MHC in Mexicans since admixture. *PLOS Genetics*, 12(2), e1005847. https://doi.org/10.1371/journal.pgen.1005847