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Review Article

Interethnic admixture and the evolution of Latin American populations

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Abstract

A general introduction to the origins and history of Latin American populations is followed by a systematic review of the data from molecular autosomal assessments of the ethnic/continental (European, African, Amerindian) ancestries for 24 Latin American countries or territories. The data surveyed are of varying quality but provide a general picture of the present constitution of these populations. A brief discussion about the applications of these results (admixture mapping) is also provided. Latin American populations can be viewed as natural experiments for the investigation of unique anthropological and epidemiological issues.

Keywords: interethnic admixture, Latin America, population structure.

The Latin American Microcosm

Geographically, Latin America extends over a vast area, from 32° North to 60° South and from 120° to 20° West of Greenwich. Within this territory, Middle America stretches from approximately 8° North to 32° North, while South America continues to the region's southern limit.

Throughout this area lives a very diverse population, inhabiting equally diverse environments with distinct geological and ecological characteristics. Tropical, subtropical, and extremely cold climates all occur in the region, along with altitude variations and moisture extremes (for example, the Atacama desert in Chile is one of the driest places in the world).

Middle America has a population of approximately 165 million people, with slightly more than half of them characterized as ethnically admixed (Mestizos). Amerindian ancestry is especially prevalent in Mexico and Guatemala, while people of African descent are more common in the Caribbean area. South America contains roughly twice as many persons (approximately 322 million), and the influence of European ancestry is more marked in this region, although interethnic admixture is as common as in Middle America.

The human populations of Latin America have been investigated from an array of disciplinary perspectives. Global evaluations of the genetics and evolution of these populations have been conducted by Salzano (1971) and Salzano and Bortolini (2002). The admixture process was considered by Sans (2000), while Gibbon *et al.* (2011) examined the ways in which ethnic identities, genetic/genomic ancestry and health interacted in Argentina, Brazil, Colombia, and Uruguay.

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Origins

General

The present Latin American populations are the consequences of a process that began in Northeastern Asia as early as 15,000-18,000 years ago (among others, Schurr and Sherry, 2004; Fagundes *et al.*, 2008; Perego *et al.*, 2009; Salzano, 2007, 2011). After the arrival of Europeans and Africans a little over five centuries ago, a complex process of admixture took place. This recent period has involved populations from a broad range of origins, making Latin American history unique (Sans, 2000). Presently, Latin America can be seen as a natural experiment for anthropological and epidemiological studies in which polymorphic loci and linkage disequilibrium can be used to infer the genetic basis for traits of interest (Chakraborty and Weiss, 1988).

The populations that entered into contact during the last several centuries were, as previously mentioned, very diverse. The original background of the region was composed by Native Americans; Europeans, mostly Spanish and Portuguese but also other nationalities; and Africans, who were initially brought to the region as slaves and came

from different areas of that continent. Some Latin American countries have also received East Indian, Chinese, Japanese, Javanese, and other Asian populations. Examples include the Japanese immigrants that came to São Paulo and Pará in Brazil or the Chinese-origin populations that initially settled in the coastal valleys of Peru and were later distributed across the whole country.

Native Americans

As indicated previously, populations originating from Asia entered America approximately 15,000-18,000 years ago, but these dates, as well as the origin or origins of these populations in Asia, are still discussed. One of the most accepted views involves a coastal route that includes a stage in Beringia, a land bridge that appeared intermittently between 70,000 and 12,000 years ago. Fagundes *et al.* (2008) suggested a complex model that involved an early differentiation from Asian populations, a slow and lengthy evolution in Beringia, and a rapid expansion in America due primarily to a maritime route and coastal settlements along the Pacific coast. This first expansion would have been followed by a terrestrial expansion through the MacKenzie corridor in North America and continued to the south by land. Other proposals, including the entrance through the Atlantic Ocean bordering Greenland, the "Solutrean solution" proposed by Stanford and Bradley (2002), and the crossing of the North pole proposed by O'Rourke and Raff (2010), cannot be rejected, but if they occurred, they most likely involved fewer migrants.

The genetic characteristics of these initial populations have not been completely identified, but several studies indicate a wide initial diversity, as seen mainly in mitochondrial DNA (mtDNA) studies (Tamm *et al.*, 2007; Fagundes *et al.*, 2008; Malhi *et al.*, 2010; Perego *et al.*, 2010; Yang *et al.*, 2010; Bisso-Machado *et al.*, 2012). Part of the initial variation could have been lost, as suggested by Cui *et al.* (2013) in an analysis of mtDNA from skeletal remains. This diversity can also be observed in the analysis of the Y chromosome (Schurr and Sherry, 2004; Bisso-Machado *et al.*, 2011, 2012). As for autosomes, a total of 678 microsatellite markers, genotyped in 422 individuals from 24 North, Central and South American natives, were studied by Wang *et al.* (2007); 364,470 single nucleotide polymorphisms were examined in 52 Native American and 17 Siberian groups by Reich *et al.* (2012). This second study indicated the presence of at least three different streams of Asian gene flow in the prehistoric colonization of the Americas, a view suggested nearly three decades ago by Greenberg *et al.* (1986).

Salzano and Bortolini (2002), based on several studies, have estimated that approximately 45 million Native Americans were living in Latin America at the beginning of the European Conquest, but projections range from 30 to 90 million. This population, however, rapidly decreased as a consequence of epidemics and the violence occurring as wars, massacres, and maltreatment (Pereña, 1992). As stated by Salzano and Callegari-Jacques (1988), native populations were in different phases of cultural and demographic development at the onset of the European Conquest. Sedentary communities in more densely populated regions suffered the structural impacts of epidemics and other factors most strongly, while many small groups became extinct. However, after this severe depopulation, Native American populations recovered, and their present numbers (approximately 63 million, unpublished estimate) are higher than in the 16th century.

Africans

Most people from Africa were forced to migrate to America due to the slave trade, but Pedro Alonso Niño, Columbus's pilot, was the first African immigrant (Brawley, 2001). As early as 1518, the Spanish crown had issued the first license for slave traffic, while Portugal had established its own companies and colonies to capture slaves. The first captives apparently entered Brazil through Bahia in 1531 (Ramos, 1934). The trade started in the Caribbean region and soon afterwards extended to Central America and the north of Brazil; its prohibition occurred over a lengthy process from 1830 to 1870.

The origins of the slaves ranged from the Guinea coast to Mozambique. Rout (1976) defined four main regions: upper Guinea, lower Guinea, the Congo Delta and Angola, and Mozambique. The flow from each of these areas varied over the long history of the slave trade and was also dependent on the nationality of the slave traders (Salzano and Bortolini, 2002).

The number of slaves brought to Latin America is difficult to determine, and factors such as slave mortality during the journey, illegal traffic, and the lack of registration due to ship interference at sea only complicate this estimation. Reader (1998) approximated that nine million slaves were shipped across the Atlantic between 1452 and 1870.

Europeans

Different processes influenced the European migrations over the five centuries after the initial contact. The first period, characterized by the arrival of the Spanish and Portuguese, was related to the Conquest. Spanish colonization was ruled by the Crown and was consequently planned as an emigration policy under royal permissions. Later, laws became more permissive due to the scarcity of migrants. This policy aimed to stimulate the migration of married settlers, farmers and artisans (Konetkze, 1991). However, because part of the migration was related to military campaigns, more men than women reached the continent. These regulations were in effect until the 18th century, when migration became independent of the Spanish government. The state was less involved and enacted fewer regulations in the immigration of the Portuguese, French, Dutch, and others to America (Konetkze, 1991).

Estimating the number of Europeans who entered Latin America is a complex undertaking. McAdoo (1993), referring to immigrants to the United States, stated that "the waves of persons who came to these shores are a portion of American history that is too often hidden away, for it embarrasses Americans," and the same statement can be applied to Latin America. Moreover, this migrant flux continued until relatively recently: the last wave occurred after World War II, and the origins of the migrants changed to include the entire Mediterranean region as well as other European countries, particularly those in Eastern Europe. It is reasonable to suggest that a new wave, involving mainly Africans and East Asians, has recently started to arrive to Latin America.

The numbers, origins and destinations of European migrants depended on the time of and reasons for the migration. For example, during the 16th century, 300,000 people belonging to different economic and social levels left Spain to come to America and spread to different parts of the continent; however, this figure refers only to travelers, not to people who remained in the continent (Konetkze, 1991). The quantity of people entering America increased quickly, and as a result, Europeans and their descendants numbered 850,000 in 1650, 13,470,000 in 1825, and 221,160,000 in 1950, according to Rosenblat (1954).

History of the Admixture Process

The admixture process started soon after Christopher Columbus first disembarked at La Hispaniola (1492), as the 39 men he left on the island had sexual intercourse with the local Native American women (Mörner, 1967). Therefore, a maximum of roughly 21 generations of admixing may be established, with some variance due to region. Wang *et al.* (2008), based on 13 mixed Latin American populations, estimated that the average time since first admixture allowed for six to 14 generations, but these estimations excluded the Caribbean region, where the process began. Based on pedigrees, Heyer *et al.* (1997) identified up to 19 generations, descended from males who lived in the 17th century.

While admixture at first involved primarily Spanish (or European) men and Native American women, it shortly expanded to include European or "criollo" (European descendants born in America) men and mixed women or mixed men and women. The process was complicated by the introduction of African slaves into America at the beginning of the 16th century. The legal status of Africans delayed their admixture with other ethnic groups, but sexual intercourse between African men and Native American or mixed women, and later between African or African-descendent women and European or criollo men, was relatively frequent (Mörner, 1967).

The social, cultural, and economic characteristics of native populations, aspects of the European Conquest and Colonization, and the nature of the Europeans and Africans arriving at the continent undoubtedly influenced the admixture process. For example, prehistoric America had great cultural and demographic heterogeneity. Salzano and Callegari-Jacques (1988) classified these populations into three stages: hunters and gatherers with incipient agriculture, with low fertility and mortality; sedentary and more advanced agriculturalists, with high fertility and high mortality; and populations living in densely inhabited areas, with high fertility and low mortality. Accordingly, the consequences of the Conquest and Colonization were different in relation to each stage; the last two were more affected by diseases and were more involved in the admixture process.

Clearly, more males than females migrated to Latin America, and the Spanish Crown encouraged unions between European men and Native American women as a way to evangelize and/or obtain economic advantages; unions between Africans and any other group were prohibited. As Mörner (1967) has stated, "In a way, the Spanish Conquest of the Americas was a conquest of women".

More recently, Latin American countries have accepted intermarriage as legal, with some exceptions; the law against marriages with Chinese in Mexico is among the most recent bans (Mörner, 1967). "Mixed blood" offspring generally became an integral part of European family life, and a long tradition of contact exists between Africans and both Spanish and Portuguese persons. Moreover, a distinct Mestizo (mixed Native American and Iberian) identity emerged in some parts of Latin America, including Mexico and Brazil (Yinger, 1985). In the latter country, interethnic unions were even favored. The Marquis of Pombal, who governed Brazil in the middle of the 18th century, established that mixed citizens should receive equal treatment as unmixed ones regarding employment, honor and dignity (Rosenblat 1954).

Individually, people from the first generation of an admixture process will have entire chromosomes of a single origin, while the second generation will have chromosomes containing blocks of different ancestry. As the process persists, these blocks of different origins will become smaller. Consequently, the chromosomes of people living in the present day show a complex mix of ancestry, depending on the number of generations of admixture, marriage patterns, and the characteristics of the mixed people involved in them.

The Genetic/Genomic Approach to Interethnic Admixture

Bernstein (1931) and Ottensooser (1944) were the first to use allele frequencies in admixed and parental populations to estimate the accumulated proportional contributions of the parental groups to a given admixed population. From that modest beginning, a vast array of methods and computing programs have been developed to analyze the problem. All of these techniques depend on two basic assumptions: (a) there is no error in the choice of parental

groups or in their genetic/genomic frequencies, and (b) the changes are due mainly to gene flow, not other evolutionary factors which may influence the estimates. Examples include those of Chakraborty (1975, 1985), who used the gene identity method to incorporate fluctuations due to the size of the hybrid population; Bertorelle and Excoffier (1998), who added the changes that may have occurred in parentals and hybrids after the event of admixture; Wang (2003), who considered gene flow after the first event of admixture; and McKeigue *et al.* (2000), who employed a Bayesian approach to incorporate the effects of linkage and population structure.

Molecular approaches now allow researchers to separate maternal and paternal contributions (mitochondrial DNA, Y chromosome); to identify variation in all DNA regions (coding and noncoding, introns, pseudogenes, repeat sequences, regulatory elements); and to determine the origin of chromosome segments depending on the ancestors' origin. The degree of divergence among alleles (Bertorelle and Excoffier, 1998; Dupanloup and Bertorelle, 2001) and the genetic drift since admixture calculated using different approaches (Bayesian: Chikhi *et al.*, 2001; maximum likelihood: Wang, 2003; and coalescence: Excoffier *et al.*, 2005) can now be considered. Molecular techniques have also improved the estimation of individual admixture, an approach initially proposed by Hanis *et al.* (1986) to avoid the variability among individuals due to recombination and independent loci assortment.

Ancestry Informative Markers (AIMs), that is, those with high discriminatory power due to large interethnic differences in frequencies, are also now being used, as suggested by Shriver *et al.* (1997, 2003) and Collins-Schramm *et al.* (2002).

Whole genome data sets are revealing complex stories of divergence and admixture that are impossible to obtain using other approaches. For example, Harris and Nielsen (2013), using parent-offspring trios from the 1000 Genomes Project, were able to detect extensive gene flow between Africa and Europe after their populations diverged; together with the ancient admixture into Europe, the results reveal a population structure that must be reconsidered to construct more realistic models of the gene pools in these regions. In a more restricted analysis, Wang *et al.* (2008) employed 678 autosomal and 29 X-chromosomal microsatellites to differentiate the Native American ancestry among Mestizos from 13 Latin American populations.

In the following sections, we provide detailed and specific information about continental ancestries. Because uniparental and X chromosome estimates generally overestimate non-European contributions, and Y chromosomes the European influence, we concentrated our attention on autosomes. With the exception of the data for Uruguay, for which we wanted to construct a complete picture, protein markers, which have been adequately surveyed in previous reviews (Sans, 2000; Salzano and Bortolini, 2002), are not considered here.

Actual Data, Middle America

Mexico

A total of 19 reports regarding molecular autosome estimates of parental continental ancestry in Mexican populations are presented in Table 1. Three of them concern the country in general, while 27 concern specific populations, with the large population of Mexico City heavily represented (seven estimates). Amerindian ancestry is most prevalent (51% to 56%) in the three general estimates, followed by European ancestry (40% to 45%); the African share represents only 2% to 5%. The Amerindian contribution is the highest in 22 (81%) of the 27 estimates.

Many cases of repeated sampling in the same population were recorded: for the general evaluations, the percentage differences are minimal (at most 6%), but for Nuevo León, Veracruz, Guerrero, and Yucatan (all sampled twice), the highest differences, generally involving the European fraction, are 17% to 28%. In Mexico City, the European contribution was estimated as 21% to 32% in six of the seven reports, with the anomalous value of 57% obtained in a single sample of 19 subjects. European ancestry is most prevalent in the north (Chihuahua, 50%; Sonora, 62%; Nuevo León, 55%), but in a recent sample from Nuevo León and elsewhere in the country, Amerindian ancestry is dominant. The general conclusion, therefore, is that the Amerindian genes were victorious in the battle of survival over those of the Spanish Conquistadores!

Other Middle American countries

Table 2 presents the Middle American data excepting those of Mexico. Clear differences may be observed between the areas: some show considerable African influence (Carib as a whole, 77%; Haiti, 96%; Jamaica, 78%-82%), others Spanish (Cuba, 73%-86%; Puerto Rico, 60%-76%, with some interregional variability; Nicaragua, 69%; Costa Rica, 58%-67%), and another Amerindian (Guatemala, 53%). In the Carib, the exception is Dominica, whose essentially trihybrid structure reflects the French (as opposed to Anglophone) influence throughout its history.

Actual Data, South America

Colombia

As shown in Table 3, the Antioquia region has been extensively studied (five Mestizo samples, one Afro-derived sample), with variable results (European fraction estimated from 46% to 79%); however, the three surveyed studies of its main urban center, Medellín, showed similar values for the European contribution (60%-66%). The two independent estimates from North Santander and Valle del Cauca are also rather similar, with lower (39%-42%) European fractions.

Table 1 - Molecular autosome estimates of parental continental ancestry in different segments of the Mexican population[1].

Type and no. of markers	Population or region	No. indiv. studied	% Ancestry			References[2]
			European	African	Amerindian	
44 AIMs	General	181	45	4	51	1
1814 AIMs	General	300	42	2	56	2
446 AIMs	General	312	40	5	55	3
	North					
13 STRs	Chihuahua	161	50	12	38	4, 5
1814 AIMs	Sonora	60	62	2	36	2
10 STRs	Nuevo León	143	55	5	40	6
74 AIMs	Nuevo León	100	38	6	56	7
1814 AIMs	Zacatecas	60	46	3	51	2
	Central					
13 STRs	General	211	52	10	38	5, 8
13 STRs	Jalisco	309	31	16	53	5, 9
1814 AIMs	Guanajuato	60	40	1	59	2
13 STRs	Hidalgo	106	25	11	64	5, 10
1814 AIMs	Veracruz	60	36	2	62	2
13 STRs	Veracruz	130	9	17	74	5
69 AIMs	Mexico City	286	30	5	65	11
15 STRs	Mexico City	378	26	5	69	12
678 STRs	Mexico City	19	57	3	40	13
128 AIMs	Mexico City	66	37	2	61	14
13 STRs	Mexico City	242	21	15	64	5, 15
550 Kb	Mexico City	984	31	3	65	16
446 AIMs	Mexico City	1310	32	4	64	17
13 STRs	Puebla	313	17	11	72	5, 9
24 AIMs	Guerrero	156	4	1	95	18
1814 AIMs	Guerrero	60	28	4	67	2
	Southeast					
1814 AIMs	Yucatan	60	39	1	60	2
13 STRs	Yucatan	262	19	11	70	5, 9
13 STRs	Campeche	106	8	16	76	5, 19

[1]As indicated, reports including uniparental markers only (for instance, Rangel-Villalobos *et al.*, 2008; Guardado-Estrada *et al.*, 2009; Salazar-Flores *et al.*, 2010; and Martinez-Cortés *et al.*, 2009) were not included.
[2]1. Chowdhry *et al.* (2006), Mexican recruited in the San Francisco Bay Area, USA; 2. Silva-Zolezzi *et al.* (2009); 3. Galanter *et al.* (2012); 4. Martínez-Gonzalez *et al.* (2005); 5. Rubi-Castellanos *et al.* (2009a); 6. Cerda-Flores *et al.* (2002); 7. Martinez-Fierro *et al.* (2009); 8. Hernández-Gutiérrez *et al.* (2005); 9. Rubi-Castellanos *et al.* (2009b); 10. Gorostiza *et al.* (2007); 11. Martinez-Marignac *et al.* (2007); 12. Juárez-Cedillo *et al.* (2008); 13. Wang *et al.* (2008); 14. Kosoy *et al.* (2009), 26 individuals from Mexico City and 40 Mexicans from California, USA; 15. Luna-Vazquez *et al.* (2005); 16. Johnson *et al.* (2011); 17. Galanter *et al.* (2012); 18. Bonilla *et al.* (2005); and 19. Sánchez *et al.* (2005).

When the specific populations from the six considered regions are examined, a wide array of continental parentage frequencies are observed, preventing an arrival at general conclusions. The same is true for the three African-derived samples, which showed African contributions ranging from 89% (Antioquia) to 46% (Mulaló). This variability may be real, but sampling biases, as well as the types and numbers of markers tested, should also be considered. New, more specific and directed investigations should be undertaken.

Brazil

Brazil is the country from which the largest number of parental ethnic estimates were obtained. Table 4 lists 13 uniparental references (mtDNA only: 1; mtDNA+Y chromosome: 4; Y chromosome only: 8), two X-linked refer-

Table 2 - Molecular autosome estimates of parental continental ancestry in different segments of the Middle American populations with the exception of Mexico[1].

Type and no. of markers	Population or region	No. indiv. studied	% Ancestry			References[2]
			European	African	Amerindian	
	Geographic regions					
105 AIMs	Eight Caribbean islands	420	15	77	8	1
	Specific populations					
13 STRs	New Providence, Bahamas	221	4	96	0	2
17 AIMs	Havana, Cuba, Spanish-descendants	79	86	14	0	3
17 AIMs	Havana, Cuba, Afro-derived	50	23	77	0	3
17 AIMs	Havana, Cuba, Mulattos	77	60	40	0	3
16 AIMs	Havana, Cuba, Random sample	129	73	26	1	4
60 AIMs	Havana and Matanzas, Cuba	584	81	16	3	5
13 STRs	Haiti	111	4	96	0	2
44 AIMs	Puerto Rico	181	60	21	19	6
15 STRs	Puerto Rico	192	76	17	7	7
93 AIMs	Puerto Rico, West	99	69	16	15	8
93 AIMs	Puerto Rico, South	75	65	19	16	8
93 AIMs	Puerto Rico, North	115	64	19	17	8
93 AIMs	Puerto Rico, Central	87	69	17	14	8
93 AIMs	Puerto Rico, Metropolitan	129	64	21	15	8
93 AIMs	Puerto Rico, East	137	55	32	13	8
93 AIMs	Puerto Rico, Total	642	64	21	15	8
13 STRs	Jamaica	119	16	78	6	2
105 AIMs	Jamaica	44	10	82	8	1
105 AIMs	St. Thomas	99	17	77	6	1
105 AIMs	St. Kitts	47	8	86	6	1
105 AIMs	Dominica	37	28	56	16	1
105 AIMs	St. Lucia	50	18	75	7	1
105 AIMs	St. Vincent	51	13	81	6	1
105 AIMs	Grenada	48	12	81	7	1
105 AIMs	Trinidad	43	16	75	9	1
678 STRs	Guatemala, East	20	40	7	53	9
15 STRs	Nicaragua	165	69	20	11	10
678 STRs	Costa Rica, Central Valley	20	67	4	29	9
39 AIMs	Costa Rica, Central Valley	1998	58	4	38	11

[1]As indicated, articles reporting protein markers (for instance, Arias *et al.*, 2002; Morera *et al.*, 2003) or uniparental markers only (Martínez-Cruzado *et al.*, 2001; McLean Jr *et al.,* 2005; Castri *et al.*, 2007; Benn Torres *et al.,* 2007; Gaieski *et al.,* 2011) were not included. No specific prevalences were given by Bryc *et al.* (2010) or Moreno-Estrada *et al.* (2013).

[2]1. Benn Torres *et al.* (2013); 2. Simms *et al.* (2008, 2010) East Asian, not Amerindian frequencies were employed in the analyses; 3. Cintado *et al.* (2009); 4. Diaz-Horta *et al.* (2010); 5. Teruel *et al.* (2011), includes individuals with dementia (40%); 6. Chowdhry *et al.* (2006); 7. Tang *et al.* (2007); 8. Via *et al.* (2011); 9. Wang *et al.* (2008); 10. Nuñez *et al.* (2010); 11. Ruiz-Narváez *et al.* (2010).

ences, and 27 references involving autosome markers. The data are subdivided into three sets: sociogeographic regions, Afro-Brazilian communities, and specific populations.

Five sociogeographic regions are generally recognized by official censuses, according to a large number of criteria, and their ethnic ancestries vary as may be generally expected from Brazilian history. More European influence is observed in the southeast and south (up to 89%), while the African contribution predominates in the northeast (maximum estimate 30%) and the Amerindian in the north (up to 19%). The center-west estimates show the highest resemblance to the northern values (Table 4).

Table 3 - Molecular autosome estimates of parental continental ancestry in different segments of the Colombian populations[1].

Type and no. of markers	Population or region[2]	No. indiv. studied	% Ancestry			References[3]
			European	African	Amerindian	
	Geographic regions					
8 AIMs	Antioquia, NW	80	79	6	16	1
11 AIMs	Antioquia, NW	80	63	11	26	2
5 *Alu* insertions	Antioquia, NW, Mestizos	34	64	17	19	3
5 *Alu* insertions	Antioquia, NW, Afro-derived	64	0	89	11	3
75 AIMs	Antioquia, NW	849	60	12	28	4
52 AIMs	Antioquia, NW	25	46	20	34	5
52 SNPs	North of Santander, NE	32	42	18	40	5
11 AIMs	North of Santander, NE	35	42	5	53	2
52 SNPs	Coffee area, CE	66	45	20	35	5
11 AIMs	Vale de Cauca, SW	124	39	22	39	2
52 SNPs	Vale de Cauca, SW	28	42	23	35	5
	Specific populations					
	Caribbean area					
11 AIMs	Cartagena	80	23	44	33	2
11 AIMs	Santa Marta	26	50	28	22	2
678 STRs	Pasto	19	39	4	57	6
	Northwest					
678 STRs	Medellín	20	66	9	25	6
11 AIMs	Medellín	80	63	11	26	2
75 AIMs	Medellín	849	60	12	28	4
678 STRs	Peque	20	37	5	58	6
11 AIMs	Peque	163	32	6	62	2
11 AIMs	Manizales	203	59	4	37	2
	Northeast					
11 AIMs	Bucamaranga	82	56	1	43	2
52 SNPs	Arauca	73	40	22	38	5
	Central					
11 AIMs	Armenia	58	57	5	38	2
11 AIMs	Bogotá	24	45	3	52	2
52 SNPs	Boyacá	80	42	20	38	5
678 STRs	Cundinamarca	19	47	2	51	6
11 AIMs	Yopal	20	24	1	75	2
52 SNPs	Huila	82	41	19	40	5
52 SNPs	Tolima	26	41	21	38	5
	Southwest					
11 AIMs	Pasto	201	32	3	65	2
11 AIMs	Popayan	61	20	23	57	2
11 AIMs	Neiva	24	39	0	61	2
52 SNPs	Huila	82	41	19	40	5
52 SNPs	Nariño	78	30	19	51	5
34 AIMs	Cauca	306	48	11	41	7
52 SNPs	Mulaló, Afro-derived	33	28	46	26	5
	Pacific coast					
11 AIMs	Quibdo, Mestizos	170	47	8	45	2
11 AIMs	Quibdo, Afro-derived	72	21	68	11	2
52 SNPs	Chocó	93	23	54	23	5

[1]As indicated, articles reporting uniparental markers only (for instance Rodas *et al.*, 2003; Yunis and Yunis, 2013) were not included. No specific prevalences were given by Bryc *et al.* (2010).
[2]NW: Northwest; NE: Northeast; CE: Central; SW: Southwest.
[3]1. Bedoya *et al.* (2006); 2. Rojas *et al.* (2010); 3. Gómez-Pérez *et al.* (2010); 4. Duque *et al.* (2012); 5. Ibarra *et al.* (2014), Porras *et al.* (2009); 6. Wang *et al.* (2008); 7. Córdoba *et al.* (2012).

Table 4 - Autosome estimates of parental continental ancestry in different segments of the Brazilian population[1].

Sampling criteria[2]	Type and no. of markers	Population or region[3]	No. indiv. studied	% Ancestry			Reference[4]
				European	African	Amerindian	
Sociogeographic regions							
		North					
1	12 STRs		253	68	14	18	1
1	28 AIMs		40	71	18	11	2
2	40 AIMs		203	70	11	19	3
		Northeast					
1	12 STRs		164	75	15	10	1
1	28 AIMs		40	77	14	9	2
2	40 AIMs		82	61	30	9	3
		Center-West					
1	12 STRs		286	71	18	11	1
1	28 AIMs		40	69	19	12	2
		Southeast					
1	12 STRs		109	75	18	7	1
1	28 AIMs		40	80	14	6	2
2	40 AIMs		264	74	19	7	3
		South					
1	12 STRs		226	81	11	8	1
1	28 AIMs		40	88	7	5	2
2	40 AIMs		189	78	13	9	3
1	48 AIMs		81	89	3	8	4
Afro-Brazilian communities							
1	3 VNTRs, 3 STRs	2 communities, N	64	18	47	35	5
1	48 AIMs	5 communities, N	103	15	69	16	4
1	48 AIMs	7 communities, N	294	29	48	23	6
1	10 AIMs	3 communities, NE	207	39	49	12	7
1	14 STRs	Marinhos, SE	60	33	67	0	8
1	48 AIMs	10 communities, SE	307	39	40	21	9
Specific populations							
1	12 STRs	Macapá, N	307	46	19	35	10
1	48 AIMs	Macapá, N	130	50	29	21	11
1	13 STRs	Belém, N	325	46	34	20	12
1	48 AIMs	Belém, N	196	54	15	31	4
1	6 VNTRs	São Luis, N	161	33	67	0	13
1	2 STRs, 2 VNTRs	São Luis, N	177	42	19	39	14
1	9 STRs	Maceió, NE	598	56	27	17	15
1	12 STRs	Brasília, CW	153	67	21	12	16
1	28 AIMs	Brasília, CW	200	77	14	9	17
1	11 STRs	Belo Horizonte, SE	234	65	34	1	18
3	3 VNTRs, 2 STRs	Rio de Janeiro, SE					
	3 blood groups	Euro-Brazilians	81	67	21	12	19
4	40 AIMs	Euro-Brazilians	107	86	7	7	20
3	3 VNTRs, 2 STRs	Afro-Brazilians	69	39	49	12	19
	3 blood groups						
4	40 AIMs	Afro-Brazilians	228	55	37	8	20

Table 4 - cont.

Sampling criteria[2]	Type and no. of markers	Population or region[3]	No. indiv. studied	% Ancestry			Reference[4]
				European	African	Amerindian	
4	46 AIMs	Afro-Brazilians	113	39	52	9	21
1	46 AIMs	General	280	59	30	11	21
		Ribeirão Preto, SE					
3	8 STRs	Euro-Brazilians	400	79	14	7	22
3	7 STRs	Afro-Brazilians	220	50	88	12	22
1	6 VNTRs	Campinas, SE	206	64	36	0	13
1	15 STRs	São Paulo, SE	294	52	34	14	24
		São Paulo, SE					
4	48 AIMs	Euro-Brazilians	367	63	22	15	27
4	48 AIMs	Afro/Euro-Brazilians	68	45	41	14	27
4	48 AIMs	Afro-Brazilians	51	32	57	11	27
1	9 STRs	Porto Alegre, S	104	86	3	11	25
1	678 STRs	Bagé and Alegrete, S	20	70	10	20	26

[1]Additional information based on uniparental or X-linked markers can be found as follows: (a) mtDNA only: Carvalho *et al.* (2008); (b) mtDNA plus Y-chromosome: RibeirodosSantos *et al.* (2002), Marrero *et al.* (2005, 2007), Hünemeier *et al.* (2007), Guerreiro-Junior *et al.* (2009); (c) Y-chromosome only: Carvalho-Silva *et al.* (2001), Ferreira *et al.* (2006), Silva *et al.* (2006), Ribeiro *et al.* (2009), Carvalho *et al.* (2010), Palha *et al.* (2011), Ribeiro *et al.* (2011), Francez *et al.* (2012); (d) X-linked only: Ribeiro-Rodrigues *et al* (2009), Resque *et al.* (2010).
[2]Key to sampling criteria: 1. Random; 2. Total ancestry, proportion of a given ancestry in a given color category multiplied by the official census information about the proportion of that color category in the specified region; 3. Morphological evaluation; and 4. Self-reported ethnicity.
[3]N: North; NE: Northeast; CW: Center-West; SE: Southeast; and S: South.
[4]References: 1. Callegari-Jacques *et al.* (2003); 2. Lins *et al.* (2010); 3. Pena *et al.* (2011); 4. Santos *et al.* (2010); 5. Vallinoto *et al.* (2003); 6. Maciel *et al.* (2011); 7. Amorim *et al.* (2011); 8. Scliar *et al.* (2009); 9. Kimura *et al.* (2013); a subset of these communities was also studied for two *Alu* insertions, and the values used to estimate parental contributions (Cotrim *et al.*, 2004), but the results obtained showed inconsistencies among the populations and were not considered; 10. Francez *et al.* (2011a); 11. Francez *et al.* (2011b); 12. Ribeiro-Rodrigues *et al.* (2007); 13. Ramos *et al.* (2004); 14. Ferreira *et al.* (2005); 15. Ferreira da Silva *et al.* (2002); 16. Godinho *et al.* (2008); 17. Lins *et al.* (2011); 18. Scliar *et al.* (2009); 19. Palatnik *et al.* (2002); 20. Suarez-Kurtz *et al.* (2007); 21. Manta *et al.* (2013); 22. Ferreira *et al.* (2006); 23. Muniz *et al.* (2008); 24. São-Bento *et al.* (2008); 25. Leite *et al.* (2003); 26. Wang *et al.* (2008); 27. Cardena *et al.* (2013).

As a result of the present emphasis of the Brazilian government on positive actions in favor of previously discriminated African-derived people, many rural areas where escaped slaves found refuge are now being demarcated to ensure property rights for their descendants. Several of these communities have been studied regarding parental markers (Table 4), and the results show high heterogeneity among them. These communities have not remained isolated from persons of other ethnic backgrounds, as illustrated by the fact that in four of the six estimates, their African contributions amount to less than half of the total parental ancestry.

Twelve specific populations are listed in Table 4. The main results can be summarized as follows: (a) repeated sampling in both Macapá and Brasília yielded less than 10% average differences; the discrepant values obtained in São Luís are most likely due to the nature and number of the markers used; (b) in Rio de Janeiro, Ribeirão Preto and São Paulo, Afro-Brazilians and Euro-Brazilians were considered separately; the sampling differences in Rio de Janeiro were not high, but the differences between Rio de Janeiro, Ribeirão Preto and São Paulo in terms of the African ancestry in Afro-Brazilians are large; and (c) differences in the specific and global regional ethnic parental estimates were most marked for São Luís [probable reason indicated in (a)].

Although in population terms the morphological and genetic/genomic evaluations generally agree, wide variability exists for individual, personal estimates. This observation should be expected due to the high frequency of interethnic unions that occurred in the past and that are likely even more prevalent in the present. The implication for the implementation of positive actions is obvious: it is impossible to establish objective, specific criteria of ethnic classification to screen potential candidates for a program. These programs must therefore rely on self-classification, disregarding possible errors in favor of the general socioeconomic improvement of the minorities considered.

Peru

The extensive study conducted by Sandoval *et al.* (2013) using 40 AIMs provides a good overall estimate of the degree of interethnic admixture present in the populations of the three main geographical regions of the country (Table 5). Overall, non-Amerindian European ancestries varied from 1% to 31%, while the African contribution was only 1% to 3%. The two coastal populations sampled contain 14% to 15% European admixture, while much lower

Table 5 - Molecular autosome estimates of parental continental ancestry in different segments of the Peruvian population[1].

Population or region	No. indiv. studied	% Ancestry		
		European	African	Amerindian
Amazon				
Andoas	71	4	1	95
Iquitos	8	2	2	96
Chachapoyas	15	5	2	93
Lamas	18	9	2	89
Pucallpa	10	8	1	91
Coast				
Lambayeque	31	15	3	82
Lima	43	14	2	84
Andes				
Cajamarma	34	21	3	76
San Marcos	19	31	2	67
Ocopon	11	4	2	94
Chogo	14	15	3	82
Huarochirí	15	2	1	97
Huancayo	29	6	3	91
Ayacucho	31	8	2	90
Kaquiabamba	9	2	1	97
Andahuaylas	19	2	1	97
Cabauaconde	20	3	1	97
Yanque	10	1	1	98
Chivay	25	2	1	97
Characato	8	24	3	73
Mollebaya	8	3	1	96
Amantani	31	1	1	98
Uros	25	2	1	97
Taquile	23	1	1	98
Anapia	24	1	1	98

[1]All of them were studied with 40 AIMs by Sandoval *et al.* (2013). It was assumed that the strictly non-European and non-African ancestries (labelled as Oceanian and East Asian) were remote ancestral Amerindian ancestries.

frequencies occur in the Amazon (2% to 9%). Some heterogeneity is observed in the Andes, with three of the four northern populations (San Marcos, Cajamarca, Chogo) presenting only 67%, 76%, and 82% Amerindian ancestry, respectively. In the extreme south, the results from Characato also show evidence of more marked admixture (73% Amerindian heritage); but the 14 other populations sampled yielded high values (90% to 98%) for Amerindian gene pools.

Argentina

Nine studies involving autosomal molecular markers were considered for Argentina, and the results are given in Table 6. For the country as a whole, the European influence (65%-79%) is dominant, but the Amerindian contribution (17%-31%) is also important. The African influence, however, is minimal (2%-4%). Considering the four geographical regions of the country, somewhat different estimates were obtained for the northeast and northwest, but the evaluations for the center and south were in general agreement.

Turning to specific populations, a geographical pattern emerges in relation to Amerindian parentage, with higher frequencies observed in the northwest and south. Within the northwest region, there is ample variability (33%-100%) of the Amerindian contribution in the Province of Jujuy, but a rough gradient of decreasing Amerindian influence is generally observed from north to south. The values in the northeast and center are similar; in the Buenos Aires megalopolis, the Amerindian percentages are modest (16%-17%) in the inner and first urban belt, but the contribution increases to 29% in the second urban belt, where migrants and people of generally low socioeconomic status live. The African contribution is low but detectable in most of the regions and populations studied, reaching its maximum in Santiago del Estero and La Rioja.

Uruguay

Uruguay is unique among Latin American countries in that it has no Native American or African-descendant communities. This fact has shaped its national identity, which at least until the 1980s was considered to be almost strictly European. This view has also affected population genetics studies. In 1986, however, the first analysis of the Mongolian spot trait showed a frequency that was much higher (42%) than that expected in a mostly European population (Sans *et al.*, 1986). This initial study encouraged additional enquiries into the Uruguayan identity. One of the first of these studies indicated that Montevideo (in the south) and Tacuarembó (in the northeast) had differences between them: while the African and Amerindian contributions in Montevideo were estimated as 7% and 1%, respectively, the same contributions in Tacuarembó were 15% and 20%, respectively (Sans *et al.*, 1997). These data demonstrated not only a clear non-European contribution to ancestry in the northeast but also population heterogeneity in this small country (176,215 km^2, 3,286,314 inhabitants, according to the 2011 National Census, INE, 2012). This estimation was based on classical (blood groups, electrophoretic proteins) markers, as was another study in Cerro Largo, in the northeast, that showed 10% Native American and 8% African ancestry contributions (Sans *et al.*, 2006). These data are in agreement with those obtained from a study using nDNA, which estimated 6% African and 10% Native American contributions for the whole country (Hidalgo *et al.*, 2005).

Studies in self-defined African descendants, however, have presented very different results: African genes contribute nearly half of the ancestry to these populations, while Native American contributions vary from 15% in the

south to 25% in the northeast and 42% in the south (Sans *et al.*, 2002, Da Luz *et al.*, 2010).

Several studies have focused on uniparental markers, especially mtDNA. The Native American maternal contri-

Table 6 - Molecular autosome estimates of parental continental ancestry in different segments of the Argentinian population[1].

Type and no. of markers	Population or region[2]	No. indiv. studied	% Ancestry			References[3]
			European	African	Amerindian	
	Geographic regions					
99 AIMs	Northeast	33	54	5	41	1
24 SNPs	Northeast	61	79	4	17	2
HLA-A, B	Northwest	1,293	55	10	35	3
99 AIMs	Northwest	37	33	3	64	1
24 SNPs	Central	153	81	4	15	2
99 AIMs	Province of Buenos Aires	263	76	4	20	1
24 SNPs	South	32	68	4	28	2
99 AIMs	South	108	54	3	43	1
99 AIMs	General	441	65	4	31	1
100 K+149 AIMs	General	94	78	2	20	4
24 SNPs	General	246	79	4	17	2
	Specific populations					
HLA-A, B	Jujuy, NW	273	47	0	53	3
8 *Alu* insertions	Jujuy, La Puna, NW	47	0	0	100	5
8 *Alu* insertions	Jujuy, Quebrada Baja, NW	36	16	7	87	5
8 *Alu* insertions	Jujuy, Quebrada Alta, NW	36	5	3	92	5
8 *Alu* insertions	Jujuy, Selva, NW	45	23	0	77	5
8 *Alu* insertions	Jujuy, Valle, NW	62	16	7	77	5
HLA-A, B	Salta, NW	241	56	3	41	3
678 STRs	Salta, NW	19	25	3	72	6
HLA-A, B	Catamarca, NW	81	53	10	37	3
678 STRs	Catamarca, NW	14	53	3	44	6
HLA-A, B	Tucuman, NW	418	67	9	24	3
678 STRs	Tucuman, NW	19	65	4	31	6
HLA-A, B	Santiago del Estero, NW	156	46	24	30	3
HLA-A, B	La Rioja, NW	124	50	19	31	3
24 SNPs	Formosa, NE	11	75	3	22	2
24 SNPs	Misiones, NE	28	83	4	13	2
24 SNPs	Corrientes, NE	21	77	5	18	2
24 SNPs	Buenos Aires, CE[4]	150	81	4	15	2
99 AIMs	Buenos Aires, inner city, CE	98	79	4	17	1
99 AIMs	Buenos Aires, 1st urban belt, CE	47	80	3	16	1
99 AIMs	Buenos Aires, 2nd urban belt, CE	22	68	3	29	1
15 STRs	Mar del Plata, CE	180	77	1	22	7
19 *Alu* insertions	Bahía Blanca, CE	119	79	0	21	8
15 STRs	Bahía Blanca, CE	85	68	4	28	7
24 SNPs	Rio Negro, S	31	68	4	28	2
9 blood polymorphisms	Puerto Madryn, S	82	68	3	29	9

[1]Earlier studies by Avena and coworkers that included protein markers only were not included here.
[2]NE: Northeast; NW: Northwest; CE: Central; S: South.
[3]1. Avena *et al.* (2012); 2. Corach *et al.* (2010); 3. Alfaro *et al.* (2005); 4. Seldin *et al.* (2008); 5. Gómez-Pérez *et al.* (2011); 6. Wang *et al.* (2008); 7. Parolin *et al.* (2013a); 8. Resano *et al.* (2007); 9. Parolin *et al.* (2013b).
[4]Using 12 autosomal markers Fejerman *et al.* (2005) estimated as 2% the African ancestry of a sample of 90 individuals from the city of Buenos Aires.

bution estimated in all of these studies is higher than that estimated by paternal genes (Y chromosome) or autosomes, reaching 62% in Tacuarembó (Bonilla *et al.*, 2004) and decreasing to 21% in Montevideo (Gascue *et al.*, 2005). For the whole country, the maternal Native American ancestry was determined as 34% (recalculated from Pagano *et al.*, 2005a). Self-identified Basque descendants with Basque paternal surnames living in Trinidad, in the southwest, also showed high levels (20%) of Native American maternal ancestry (Sans *et al.*, 2011). The African contribution is relatively less, but the maternal contribution of this ancestry was estimated as 17% in Tacuarembó (Bonilla *et al.*, 2004) and 21% in Cerro Largo (Sans *et al.*, 2006). Self-defined African descendants presented 52% African and 29% Native ancestry (Sans *et al.*, 2002). Y-chromosomal data indicated much lower African (less than 1%) and Native American (less than 8%) contributions (Bertoni *et al.*, 2005, Pagano *et al.*, 2005b).

Genealogical data have also been used to better understand parental contributions for Basque descendants (Sans *et al.*, 2011), people from Santo Domingo de Soriano in the west (Barreto, 2011), and Canarians in Canelones, close to Montevideo (Barreto, 2008).

Recently, genetic or multifactorial diseases related to or influenced by ethnic ancestry have attracted attention. For hemoglobinopathies, the presence of 0.8% (2.2% in individuals with declared African ancestry) HbS, 1.2% of the $-\alpha^{3.7}$ mutation in α-thalassemia, and 0.25% of the β^0 codon 39 β-thalassemia in Montevideo indicated the influence of African and Mediterranean ancestries (Da Luz *et al.*, 2013). Other diseases for which gene frequencies are being investigated are diabetes (Mimbacas *et al.*, 2004), breast cancer and melanoma (Cappetta *et al*., unpublished, and studies in progress).

The genetic studies performed in Uruguay have had two important outcomes. First was their contribution to the change in Uruguayan national identity, a process that started in the 1980s based on historical, demographic, and anthropological information (Verdesio, 1992; Viñar, 1992; Demasi, 1995), as well as ethnic movements (associations such as "Mundo Afro" or "Asociación de Descendientes de Indígenas Charrúas," both founded in 1989, and others, which appeared more recently). This "new" identity currently relates Uruguay to other Latin American countries rather than to Europe exclusively (Sans, 2011). Second was their contribution to the search for diseases associated with non-European ancestries, linking alleles to population origins. This latter contribution is now demonstrating its full potential, and ancestry studies are being incorporated to bolster analyses of disease presence, frequency and prognosis.

Other South American countries

The results for three previously undiscussed South American countries are displayed in Table 7. For Venezuela, the data of the geographic regions indicated a basically trihybrid distribution, with similar contributions of European, African and Amerindian parentages. However, differences emerge when specific populations are considered, with higher (52% to 73%) European fractions. The exception is an African-derived isolate in the state of Zulia (100% African). Additionally, a sample from people of lower socioeconomic status in Caracas shows higher frequencies of African and Amerindian parentages than one from people of a higher socioeconomic level (27% vs 8% and 40% vs 17%, respectively). This result reflects the stratification that has occurred over centuries of ethnic discrimination across Latin America. Two samples from Ecuador show a high (73%) Amerindian contribution to Mestizos, while the Afro-derived subjects present only an approximately half (56%) African parentage. The two Chilean populations surveyed indicate a basically dihybrid (European/Amerindian) composition.

Actual data - Overview

The data surveyed generally confirm previous historical and nonmolecular evaluations. A marked Amerindian influence exists in Mexican, Guatemalan, Peruvian, and Ecuadoran populations, while European ancestries are more prevalent in Cuba, Puerto Rico, Nicaragua, Costa Rica, Argentina, and Uruguay. For Venezuela, the European, Amerindian, and African fractions are similar, while for Colombia, high interpopulation variability is observed. The ethnic distribution in Brazil follows a geographical pattern, with European influence more prevalent in the southeast and south, African in the northeast, and Amerindian in the north. For Chile, the Amerindian and European contributions are equivalent.

The data from which these general conclusions were obtained, however, are uneven and of varying quality. The following problems were noted: (a) dissimilar amounts of coverage for the different countries, some of which were not represented at all; (b) sample representativeness in nature and size; (c) types and number of markers used; (d) phenotypic characterization of the subjects sampled; and (e) methods of quantitative ancestry determination. Only a systematic, comprehensive approach, ideally involving multinational teams of researchers, will yield a more detailed picture of the highly complex process of admixture and its social implications.

Application - Admixture Mapping

Continental parentage estimates are not only of historical interest. Admixture mapping is a tool that is increasingly being used to localize disease genes in populations of recently mixed ancestry in which the ancestral populations have differing genetic risks. For example, Native American and Latino populations show higher frequencies for type 2 diabetes, obesity, gallbladder disease, and rheumatoid arthritis, as well as lower prevalences for asthma and prostate

Table 7 - Molecular autosome estimates of parental continental ancestry in populations from three South American countries[1].

Type and no. of markers	Population or region[2]	No. indiv. studied	% Ancestry			References[3]
			European	African	Amerindian	
	Venezuela					
	Geographic regions					
9 STRs, blood groups	Northern-Central	106	38	38	24	1
2 STRs, blood groups	Central-Western	105	59	16	25	1
	Specific populations					
3 STRs, 1 VNTR, blood groups	Churuguara, NW	60	52	28	20	2
7 STRs	Isla de Toas, NW	232	63	11	26	3
7 STRs	Maracaibo, NW	246	73	4	23	3
	Caracas, NC					
3 STRs, blood groups	High socioeconomic level	60	75	8	17	4
3 STRs, blood groups	Low socioeconomic level	50	33	27	40	4
7 STRs	San José de Heras, NW	94	0	100	0	3
15 STRs	Ecuador, Mestizos	102	19	8	73	5
15 STRs	Ecuador, Afro-derived	94	16	56	28	5
678 STRs	Chile, Paposo	20	42	2	56	6
678 STRs	Chile, Quetalmahue	20	49	1	50	6

[1]As indicated, articles reporting uniparental markers only (for instance, Cifuentes *et al.*, 2004; Castro de Guerra *et al.*, 2011; Gómez-Carballa *et al.*, 2012) were not included. No specific prevalences were given by Bryc *et al.* (2010).
[2]NE: Northeast; NW: Northwest; NC: Northern-Central.
[3]1. Simmons *et al.* (2007); 2. Acosta Loyo *et al.* (2004); 3. Zabala Fernandez *et al.* (2005); 4. Martínez *et al.* (2007); 5. González-Andrade *et al.* (2007); 6. Wang *et al.* (2008).

cancer, in comparison to populations of European ancestry (Price *et al.*, 2007; Winkler *et al.*, 2010).

This method has both advantages and disadvantages in comparison to dense, whole-genome scans. The advantages include (a) lower genotyping costs; (b) the use of disease cases only, avoiding the noise introduced by inadequate controls; and (c) the characteristics of the admixture signal, which reduce the number of hypotheses tested. The disadvantages include (a) possible differences between the estimated ancestry and the frequencies of a given disease allele; (b) imperfect power to estimate local ancestry; and (c) the need for the fine mapping of the fraction of admixture that successfully identifies a disease locus.

Panels for these analyses involving Mexican Americans have been developed by Collins-Schramm *et al.* (2004; 100 AIMs) and Tian *et al.* (2007; 5,287 AIMs), and similar panels have been developed for Hispanic/Latino populations in general by Price *et al.* (2007; 1,649 AIMs) and Mao *et al.* (2007; 2,120 AIMs). Examples of the specificity of this approach include: (a) Price *et al.* (2007), who estimated that in Latinos and Mexicans from Los Angeles, where Native American ancestry is close to 50%, admixture mapping should be 15% to 30% more powerful per sample than in Colombians or Brazilians, who have lower percentages of this ancestry; and (b) Fejerman *et al.* (2012), who identified a region in chromosome 6 related to breast cancer susceptibility in Latinas. A detailed review of the studies in this area, however, is outside the scope of the present work.

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