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Surnames in Gracias a Dios: Population structure and residence patterns in the Honduran miskito territory assessed through isonymy

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ABSTRACT

The main objective of this paper is to assess the genetic structure and residence preferences of the populations that inhabit the Honduran Moskitia, a wide area of tropical rain forest that comprises the Department of Gracias a Dios, in the republic of Honduras. For this purpose, common isonymy parameters within and between parishes, as well as residence patterns using both surnames were calculated from a list of 22,961 electors at 54 villages or towns, grouped in six municipalities. High Isonymy values were obtained from all the communities and predominance in patrilocality in most of them, revealing a highly structured, patrilocal population composed mainly by relatively isolated communities. Analysis of isonymy between communities revealed the most probable historical migration routes and relations among locations. Evidence of an early relatively homogeneous peopling of the region followed by high differentiation between communities was found. The findings suggest that the Department of Gracias a Dios is a structured population composed mostly by communities with high endogamy and genetic drift, which makes it suitable for the performance of genetic studies on mendelian or complex diseases. The capital city of the department, Puerto Lempira, may be the only one experiencing a fast urbanization process. © 2011 Trade Science Inc. - INDIA

KEYWORDS

Honduran Moskitia;
Genetic isolate;
Surnames;
Genetic structure;
Urbanization.

INTRODUCTION

The identification of isolated human groups may result convenient for medical genetics, as for instance, prior to studies on complex trait loci or Mendelian diseases. Founder events produced upon foundation of towns and genetic drift in small populations change allelic frequencies and thus, could increase susceptibility genetic variants that might be otherwise difficult to detect in large, urban populations through allelic association studies.

It may be convenient to consider multiple populations when searching for candidate genes in complex diseases[1, 2], and rural populations might be adequate for this type of studies due to the high linkage disequilibrium and genetic homogeneity observed in them[3, 4].

High inbreeding increases the proportion of homozigous loci, and consequently the proportion of inherited recessive disorders[5, 6]. The effects of several factors, as migrations, inbreeding, and consanguinity avoidance through an approach based on the analysis of surnames (namely isonymy) can offer important insights in the assessment of population dynamics and genetic structure of isolates that could aid in designing biomedical and genetic studies[7-11].

The Honduran Miskito territory, or Honduran Moskitia, is a wide area (16,630 Km^2) of tropical rain forest spanning the Department of Gracias a Dios in Honduras, which comprises several protected natural habitats including the Plátano River biosphere reserve, the wildlife refuges of Caratasca and Guaimoreto lagoons, and the Kruta River biological reserve. Its human population is dispersed, forming small, rural villages, all of which are located close to rivers, lagoons or the Caribbean coast. The Capital city, Puerto Lempira, is a multicultural center with the largest population of the region. The population of the Honduran Moskitia is comprised mostly by the Miskito ethnic group, an admixture of Black Africans, Amerindians, British and Spaniards. Other groups inhabiting the area, although in small numbers, are the Tawahkas, the Pech (both Amerindian), the Garífuna (Afro-descendant) and the Ladinos (admixture of Spaniards, Amerindians and/or Black Africans without a clear ethnic affiliation)[12].

It is believed that the Miskito merged in the 17th Century, when two ships carrying Black African Slaves wrecked near the Cape of Gracias a Dios, in the Central American continental Caribbean coast. The Black Africans admixed with Native Amerindians (Tawahkas) descendants of South American Chibchas. The new ethnic group came to be the Zambo-Miskito (or Miskito, solely). From Cape of Gracias a Dios the population expanded, dominating other indigenous groups and peopling the coast and river shores of what is now called the Honduran and Nicaraguan Moskitia[13]. Although this is the most accepted hypothesis, the origin of the group might have been rather complex[14]. In addition to African and Indigenous ancestry, other minor contributions to the Miskito genetic pool include English, Spanish, Creole, Carib, Syrian and Chinese[15].

The existence of some spatial differences in the genetic composition in Miskitos has been proposed: stronger Black African influences in the populations to the north, near Cape of Gracias a Dios and throughout the coast, and a preponderance of American Indigenous contribution to the South, reflecting the geographical location of the shipwreck[13]. It is possible that the confluence with the Garífuna ethnic group in the west of the department[16] might have raised the African component.

In the 17th and 18th Centuries the Englishmen, in their struggles against the Spaniards for the domination of the Caribbean territories, established good relations with Miskitos. In that time an important English gene flow into the Miskito group might have taken place[17]. In 1786 Spain and England signed a treaty forcing the latter to abandon Honduran territory[12]. Since then Spanish genetic and cultural influences, which may include bestowing of surnames, have predominated. At present, there is some genetic and phenotypic evidence of the predominance of the Indigenous component in Miskitos, assessed from a study in a population from Nicaragua[18]; however, information regarding the adoption or transmission of surnames in the initial admixed populations in the region is scarce.

The aim of this paper is to determine the structure of the communities that compose the Honduran Miskito Territory, the relatedness among them, and the predominant residence patterns of their inhabitants by an approach based on Isonymy. Several papers have been published presenting allelic frequencies of forensic autosomal DNA markers in Honduran general population[19] and in Garífuna populations that inhabit the Caribbean coast of the country[16, 20]; nonetheless, no studies on the structure of the communities of the Honduran Moskitia using surnames or genetic markers have been published to this day.

MATERIALS AND METHODS

Sample

The lists used for the analysis of surnames were taken from the database of the national electoral office of Honduras. Surnames of 22,961 electors over 18 years old, at 54 villages or towns, grouped in the six municipalities of the Department of Gracias a Dios were

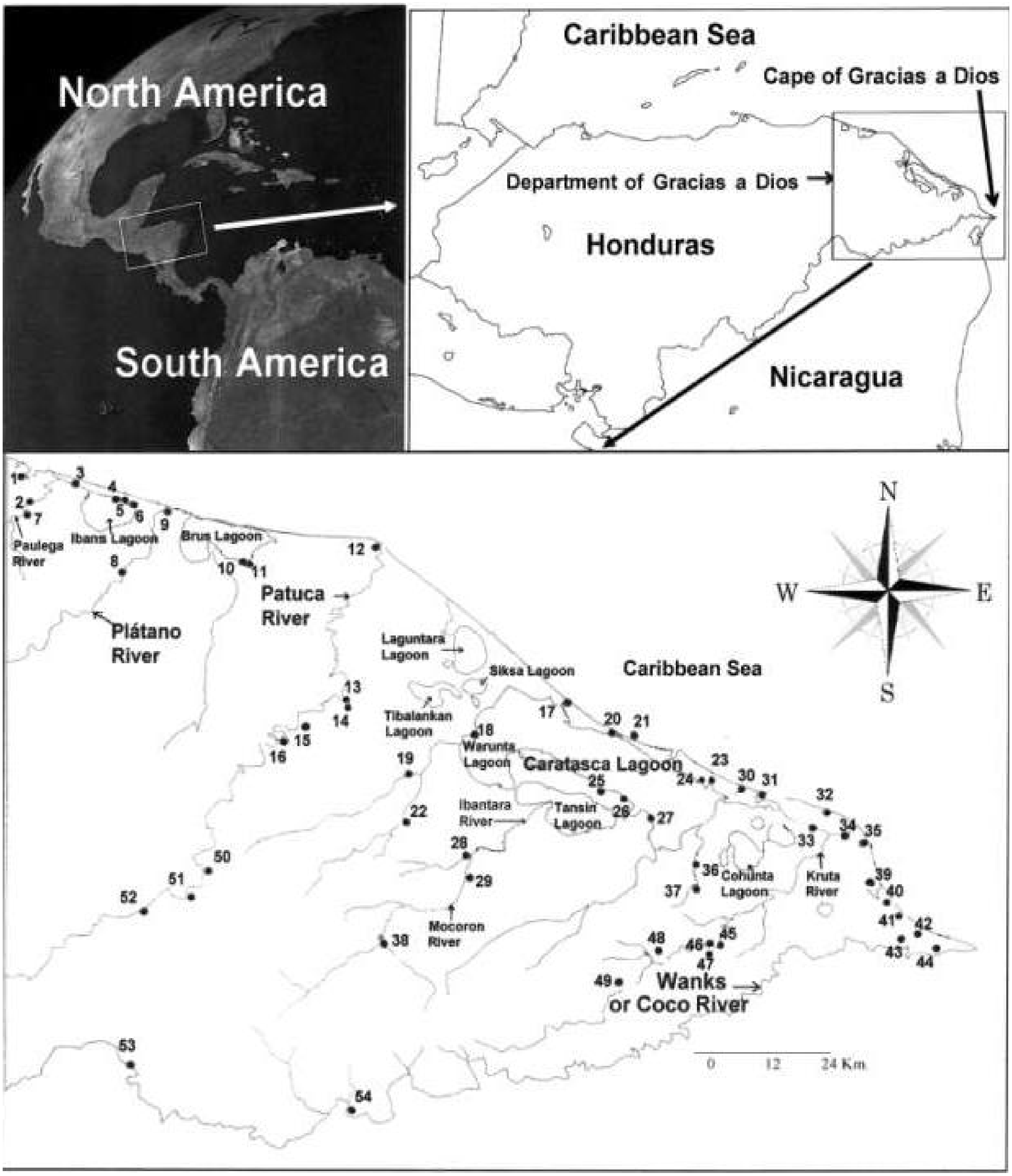

Figure 1 : Map of the Department of Gracias a Dios. Names of main rivers and lagoons are shown. Numerated dots represent the communities under study: 1.Batalla, 2.Palacios, 3.Plaplaya, 4.Ibans, 5.Cocobila, 6.Belén, 7.El Limonal, 8.Las Marías, 9.Río Plátano, 10.Tuitanta, 11.Brus Laguna, 12.Barra Patuca, 13.Paptalaya, 14.Ahuas, 15.Wasma, 16.Wawina, 17.Uji, 18.Aurata, 19.Warunta, 20.Krata, 21.Yahuabila, 22.Cocodakra, 23.Dapat, 24.Prunitara, 25.Palkaka, 26.Tasbarraya, 27.Puerto Lempira, 28.Wawplaya, 29.Sirsitara, 30.Halavan, 31.Tailibila, 32.Yamanta, 33.Kanko, 34.Kruta, 35.Usibila, 36.Laka Tabila, 37.Tuntuntara, 38.Mocorón, 39.Pakui, 40.Benk, 41.Raya, 42.Clupki, 43.Mangotara, 44.Iralaya, 45.Tikua, 46.Kuri, 47.Tikiraya,48.Tipilalma, 49.Auka, 50.Wampusirpi, 51.Krausirpi, 52.Tukrun, 53.Ahuasbila, 54.Suji.

analyzed (see Figure 1 for geographic locations).

Isonymy, F_{ST} and Fisher's α within communities

In Honduras as in most Latin America two surnames are used (the first one strictly patrilinealy transmitted and the second one inherited from the mother). Random isonymy, which is roughly four times the inbreeding coefficient F_{ST}, was calculated by the method first described by Crow & Mange extended to include both surnames[21]. The estimation of random isonymy from both surnames in the present generation may be equivalent to its estimation from marriage dispensations in the prior generation. Briefly, random component of isonymy (I) within a given territory or subdivision would be $\Sigma_i P_i^2$, where P_i is the frequency of surname i. Jorde & Morgan noted that this expression applied to the pooled databases of first and second surnames (databases of males' surnames and females' surnames in the case of marriage dispensations) is essentially equivalent to $\Sigma_i P_i Q_i$, where P_i is the frequency of surname i in the database of first surnames, and Q_i is the frequency of surname i in the database of second surnames[22].

Fisher's α is a measure of the effective number of surnames, and is calculated as the inverse of I[23-26]. High values for α would be observed in communities with high immigration, whereas low values would correspond to isolated communities with high genetic drift.

Additional parameters used as measures of surname diversity include estimators B and C, which are the proportions of the seven and the fifteen most frequent surnames, respectively[10]. High values for these estimators would be obtained in isolated communities where few surnames repeat in a high percentage of the population.

Isonymy between communities

This measure depends on surname sharing among i and j communities and is a function of the kinship between them[27]. It is calculated as $I_{ij}=\Sigma_k P_{ki} P_{kj}$, where P_{ki} and P_{kj} are the relative frequencies of surname k in the ith and jth community, respectively. For the estimations, the lists of pooled first and second surnames were used. A high value would be observed in case of two communities with short splitting time from common ancestral origin and/or high migration rates among both. Calculations were performed over the community and municipality levels. Here, Isonymy between communities will be sometimes referred to as 'Isonymyc relations' or 'relations' solely. Lasker's distance was calculated from values of isonymy as $L=-(\log I_{ij})$[27].

It is worth to say that interpretation of isonymy between and within populations rely on various assumptions that are rarely accomplished in real human populations. These assumptions include, but are not limited to, monophyletic surname origins and minimal changes due to name changes (mutations). Effects of violations of these assumptions may vary from work to work, lowering the confidence of the kinship calculations; nevertheless, the information may be useful in a comparative manner within a given territory[28]. For a review on isonymy see reference 29 and references therein.

Residence patterns

Sex-specific differences in migration rates are expected in matrilocal and patrilocal societies. Uxorilocal residence (i.e. matrilocality) implies that women remain in their natal villages after the marriage, whereas the opposite occurs in virilocal (i.e. patrilocal) groups. Differences in migration rates would be reflected on variability of sex-specific markers[30, 31]. Similarly, in countries in which two surnames are used, differences in random isonymy values between first and second surnames may reflect residence patterns (and hence, differences in migration rates between men and women) in the parental generation. Some authors have taken advantage of this fact to obtain reliable values of isonymy and to assess residence patterns[16, 32, 33]. Higher random isonymy values for first surnames compared to second surnames would correspond to patrilocality, and lower values, to matrilocality. Percentages of the two alternative residence patterns (relative to each other) in each village or town were estimated using random isonymy calculated separately from each (first and second surnames) list. Briefly, patrilocality was calculated as $(I1SN/(I1SN+I2SN))$X100, and matrilocality as $(I2SN/(I1SN+I2SN))$X100, where $I1SN$ and $I2SN$ are the random isonymies estimated for first and second surnames respectively. It is important to emphasize that this approximation may provide information on residence patterns in the parent's generation only, and it is useless (by itself) to determine historical differential migrations, or historical shifts in type of residence.

In Honduras, natural persons (i.e. with only one surname) are those not recognized by their fathers, and therefore, inherit their surname from their mothers. In order to avoid additional bias in patrilocality and matrilocality estimations, electors with only one surname were excluded from all analyses. Fortunately, the number of such cases of illegitimacy in the lists of voters was rather low (˜1.5%). Analyses were performed for the three hierarchical levels: communities, municipalities and overall department.

RESULTS

A grand total of 4,057 different surnames were found in the pooled list of first and second surnames in Gracias a Dios. TABLE 1 shows the 50 most common surnames and their occurrence in the overall department, as well as in each municipality. The 10 most frequent surnames are all of Spanish origin, with the exception of Wood, which occupies de 7th place. Of the 50 different surnames in the list, 14 (28%) are of English origin.

Some surnames probably originated in Honduran territory, such as 'Honduras' and 'Tela'. The first and second most frequent surnames in Gracias a Dios (Martinez and López) are the fourth and third most frequent in Western Europe, respectively, whilst the most frequent in Western Europe (García) is the sixth in Gracias a Dios (a list of the most frequent surnames in Western Europe can be found in reference 34).

Singletons (i.e. those surnames occurring once in the database) were found in a proportion of 0.0459. The locality with the highest proportion of singletons is Puerto Lempira City, with 0.0973. Many of these singletons are probably mutations due to errors in transcription at the people registry. For instance, Allan and Allin, both singletons, may be mutant derivatives of Allen (with an occurrence of 139 in the whole database). Moreover, many transcription errors might have propagated in the population in past generations, raising the diversity of surnames, resembling a process of increased genetic differentiation by mutation that may lead to an overestimation of genetic diversity. This mechanism of surname diversification was found to be frequent in Gracias a Dios. As an example, the surname 'Beneth' (n=203) might have mutated to the forms Benett (n=19),

TABLE 1 : Fifty most frequent surnames in the pooled lists of first and second surnames in overall Gracias a Dios, and their occurrence in each municipality

Surname	Overall	PL[a]	A[b]	BL[c]	JFB[d]	VM[e]	W[f]
MARTÍNEZ	1066	375	111	179	218	88	95
LÓPEZ	1005	345	252	231	104	51	22
FLORES	756	459	40	70	28	67	92
GÓMEZ	520	403	29	45	16	12	15
ZELAYA	497	124	102	77	39	10	145
GARCÍA	449	331	38	25	11	27	17
WOOD	424	103	20	287	4	7	3
ÁLVAREZ	419	184	16	122	81	7	9
GONZALES	416	161	36	97	63	3	56
PEREZ	385	168	14	18	15	156	14
CRUZ	358	82	18	55	20	5	178
ORDOÑEZ	356	99	181	25	1	3	47
COOPER	334	231	34	59	0	1	9
PAISANO	312	52	37	206	10	6	1
MEJÍA	281	101	8	99	58	7	8
HAYLOCK	268	255	4	2	0	7	0
RODRIGUEZ	250	71	46	31	38	38	26
PADILLA	245	139	2	9	9	82	4
RONAS	245	112	29	81	15	7	1
MENDOZA	242	51	15	7	9	76	84
WILSON	240	81	41	71	4	9	34
HERNANDEZ	239	47	2	36	78	5	71
WILLIAMS	239	128	21	5	13	69	3
WALDAN	237	34	24	2	0	133	44
RICHARD	232	218	0	2	2	10	0
TRAPP	229	32	43	144	2	7	1
CALDERON	213	100	9	4	3	79	18
REYES	213	117	39	36	7	8	6
SAMBOLA	212	196	2	0	0	14	0
MORALES	208	96	22	11	20	59	0
BENETH	203	108	8	85	0	1	1
GUTIERREZ	200	105	41	9	42	1	2
MENDEZ	188	120	21	13	6	21	7
SANCHEZ	184	37	2	5	11	6	123
THOMAS	184	48	7	40	69	19	1
SUAZO	181	87	2	10	77	1	4
ROSALES	178	73	13	16	5	54	17
BALDERRAMOS	175	36	94	11	1	27	6
NIXON	175	138	25	5	1	4	2
TAYLOR	175	81	24	33	1	35	1
MARCELO	170	162	4	3	0	1	0
BROWN	168	146	13	3	2	4	0
GREEN	167	94	5	2	52	14	0
FERRERA	165	11	93	54	2	1	4
SMITH	160	65	36	45	9	5	0
ZUNIGA	160	43	2	51	2	53	9
VALERIANO	160	37	9	105	7	1	1
MILLER	154	22	10	118	1	3	0
SALAZAR	154	84	40	18	3	6	3
TELA	153	92	0	17	3	34	7

Puerto Lempira, Ahuas, Brus Laguna, Juan Francisco Bulnes, Villeda Morales, Wampusirpi

TABLE 2 : Parameters calculated from surnames in 54 communities at 6 municipalities of the Department of Gracias a Dios (Honduran Moskitia)

Community	N[g]	ND1S[h]	ND2S[i]	TNDS[j]	*I*[k]	FST[l]	α[m]	P[n]	M[o]
Ahuasbila[a]	135	79	83	29	0.01435	0.00359	70	49.46%	50.54%
Suji[a]	332	142	133	221	0.01706	0.00426	59	44.55%	55.45%
Mocorón[a]	502	163	186	274	0.01425	0.00356	70	51.88%	48.12%
Cocodakra[a]	397	151	176	268	0.01817	0.00454	55	58.69%	41.31%
Wawplaya[a]	89	40	47	74	0.05093	0.01273	20	46.43%	53.57%
Sirsitara[a]	261	111	108	175	0.02077	0.00519	48	50.39%	49.61%
Aurata[a]	133	59	75	113	0.03027	0.00757	33	65.95%	34.05%
Uji[a]	363	124	129	197	0.02141	0.00535	47	51.76%	48.24%
Tansin (Tasbarraya)[a]	511	169	167	268	0.03286	0.00821	30	41.74%	58.26%
Palkaka[a]	375	134	140	213	0.01857	0.00464	54	50.93%	49.08%
Auka[a]	676	177	195	297	0.02459	0.00615	41	53.03%	46.97%
Krata[a]	497	185	190	307	0.01623	0.00406	62	46.22%	53.79%
Yahurabila[a]	306	135	155	244	0.01235	0.00309	81	54.45%	45.55%
Puerto Lempira City[a]	3072	771	913	1235	0.00429	0.00107	233	59.62%	40.38%
Tipilalma[a]	374	158	167	258	0.01405	0.00351	71	46.84%	53.16%
Laka Tabila[a]	610	180	202	305	0.02105	0.00526	48	40.39%	59.61%
Tuntuntara[a]	269	108	121	186	0.02351	0.00588	43	53.94%	46.06%
Prunitara[a]	247	100	112	180	0.02489	0.00622	40	54.23%	45.77%
Kuri[a]	320	128	144	210	0.01651	0.00413	61	48.56%	51.44%
Tikiraya[a]	444	136	161	246	0.03029	0.00757	33	55.82%	44.18%
Dapat[a]	488	169	203	300	0.01787	0.00447	56	61.75%	38.25%
Tailibila[a]	153	82	88	143	0.02649	0.00662	38	45.41%	54.59%
Tikua[a]	144	85	98	161	0.01676	0.00419	60	59.71%	40.29%
Kanko[a]	109	59	61	96	0.02609	0.00652	38	56.68%	43.32%
Yamanta[a]	104	45	55	80	0.02972	0.00743	34	55.78%	44.22%
Halavan[a]	310	138	151	235	0.02137	0.00534	47	72.35%	27.65%
Brus Laguna[b]	1175	336	328	516	0.01345	0.00336	74	50.79%	49.21%
Barra Patuca[b]	909	222	252	369	0.02261	0.00565	44	51.21%	48.79%
Belén[b]	318	130	126	205	0.01289	0.00322	78	44.01%	55.99%
Cocobila[b]	339	115	118	181	0.02082	0.00521	48	46.92%	53.08%
Las Marías[b]	172	75	82	129	0.02287	0.00572	44	51.30%	48.70%
Río Plátano[b]	425	137	164	244	0.01518	0.00379	66	53.77%	46.23%
Tuitanta[b]	286	114	117	190	0.0383	0.00958	26	58.77%	41.23%
Ahuas[c]	659	233	238	360	0.0125	0.00312	80	52.61%	47.39%
Paptalaya[c]	636	177	213	300	0.01616	0.01608	16	53.47%	46.53%
Wawina[c]	630	165	192	281	0.02746	0.00686	36	46.66%	53.34%
Wasma[c]	299	92	83	138	0.03277	0.00819	31	44.95%	55.05%
Batalla[d]	535	114	112	167	0.0284	0.0071	35	50.01%	49.99%
Ibans[d]	491	165	183	273	0.01823	0.00456	55	50.78%	49.22%
Palacios[d]	378	140	148	220	0.01361	0.0034	73	46.29%	53.71%
Plaplaya[d]	269	107	105	163	0.02362	0.00591	42	51.06%	48.95%
El Limonal[d]	134	64	76	115	0.02498	0.00624	40	53.60%	46.40%
Raya[e]	510	97	196	324	0.01159	0.0029	86	49.79%	50.21%
Benck[e]	350	126	130	208	0.01956	0.00489	51	46.25%	53.75%
Clupki[e]	225	68	69	111	0.05659	0.01415	18	55.57%	44.43%
Kruta o Walpatara[e]	359	140	143	224	0.02321	0.0058	43	44.82%	55.18%
Iralaya[e]	321	109	119	186	0.01989	0.00497	50	54.43%	45.57%
Usibila[e]	194	71	75	115	0.04258	0.01064	23	49.01%	50.99%
Mangotara[e]	191	81	90	139	0.01682	0.0042	59	52.65%	47.35%
Pacui[e]	195	81	84	138	0.02101	0.00525	48	51.80%	48.20%
Wampusirpi[f]	791	209	214	336	0.01856	0.00464	54	49.49%	50.51%
Krausirpi[f]	422	92	96	146	0.04143	0.01036	24	54.95%	45.05%
Tukrun[f]	427	109	109	170	0.02912	0.00728	34	52.06%	47.94%

Puerto Lempira, Brus Laguna, Ahuas, Juan Francisco Bulnes, Villeda Morales, Wampusirpi, Number of users, Number of different first surnames, Number of different second surnames, Number of different surnames, Isonymy within locations calculated from the pooled lists of first and second surnames, Inbreeding coefficient calculated from isonymy, Fisher's α, Patrilocality, Matrilocality

TABLE 3 : Parameters calculated from surnames in the 6 municipalities of the Honduran Moskitia

Community	N	ND1S	ND2S	TNDS	*I*	FST	α	P	M
Puerto Lempira	11221	1612	1974	2653	0.00382	0.00096	262	53.25%	46.75%
Brus Laguna	3624	641	729	1037	0.00870	0.00218	115	52.79%	47.21%
Ahuas	2324	462	529	749	0.01042	0.00261	96	52.14%	47.86%
Juan Francisco Bulnes	1807	363	401	568	0.01153	0.00288	87	47.14%	52.86%
Villeda Morales	2345	533	583	869	0.00724	0.00181	138	51.50%	48.50%
Wampusirpi	1640	302	298	465	0.01659	0.00415	60	52.21%	47.79%
Mean (unweigthed)	3827	652	752	1057	0.00972	0.00243	126	51.27%	48.73%
Overall	22961	2447	2997	4057	0.00366	0.00092	273	53.13%	46.87%

Benet (n=15), and Beneht (n=3). While some authors have solved the problem of mutations by merging similar surnames into a single one[35], doing so in Gracias a Dios would be a complex and confusing task due to the abundance of this phenomenon, complicating rather than simplifying the analysis.

Common parameters inferred from first, second and pooled surnames in 54 communities of the Honduran Moskitia are shown in TABLE 2. The highest random Isonymy value corresponds to the village of Warunta (ID code in Figure 1 = 19). We note that all communities, with the exception of Puerto Lempira (*I*=0.00429), show values of random isonymy over 0.01, and most over 0.02, which might be a consequence of high genetic drift and/or endogamy. TABLE 3 shows parameters for the municipality level. In all municipalities, with the exception of Juan Francisco Bulnes, patrilocality predominates (higher values for random isonymy from first surnames when compared to values from second surnames).

The ten most isolated communities in Gracias a Dios are shown in TABLE 4. For these communities, unweighted mean random isonymy (UMRI) was 0.0420, while this value is reduced to 0.0236 for the 54 localities. UMRI for the municipality level was lower (0.0097), revealing some degree of differentiation between municipalities. To further investigate the main source of differentiation within the territory (among localities or among municipalities), analyses of variance for each municipality and for the whole department were performed. In all cases, variances for locality level (in each municipality) were higher than variance for municipality level (data not shown), consistent with an early, relatively homogeneous distribution of surnames in the territory, followed by a high local differentiation due to genetic drift and high endogamy.

High correlations between different measures of surname diversity were found. Particularly, distribution of values of estimator B appears to be a potential function of random isonymy (Figure 2).

TABLE 4 : Ten most isolated communities in Gracias a Dios

Community	*I*	Estimator B	Estimator C
Warunta	0.0643	0.5400	0.6850
Clupki	0.0566	0.5133	0.6378
Wawplaya	0.0509	0.4278	0.5889
Usibila	0.0426	0.4510	0.6031
Krausirpi	0.0414	0.4491	0.6540
Tuitanta	0.0383	0.3322	0.4476
Tansin(Tasbarraya)	0.0329	0.3425	0.4618
Wasma	0.0328	0.3645	0.5602
Tikiraya	0.0303	0.3547	0.5000
Aurata	0.0303	0.3684	0.5075

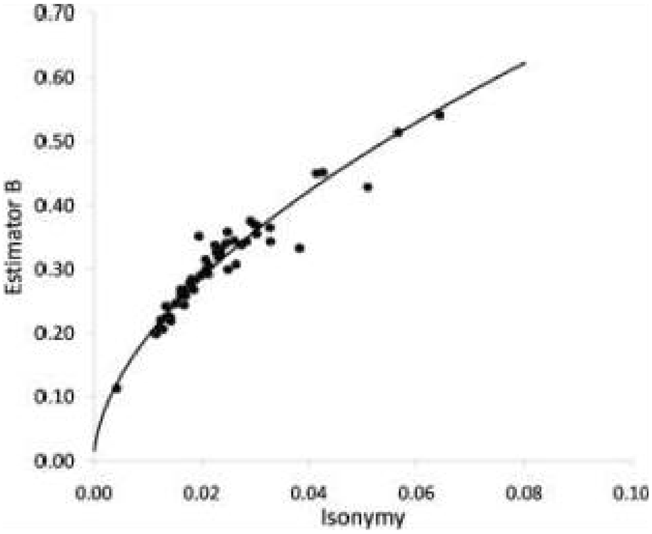

Figure 2 : Dispersion graph of values of estimator B (Y axis) and random isonymy (X axis). Estimator B appears to be a function of random isonymy. The equation that best fits the dispersion is $B=2.5595I^{0.5599}$ ($R^2=0.9361$).

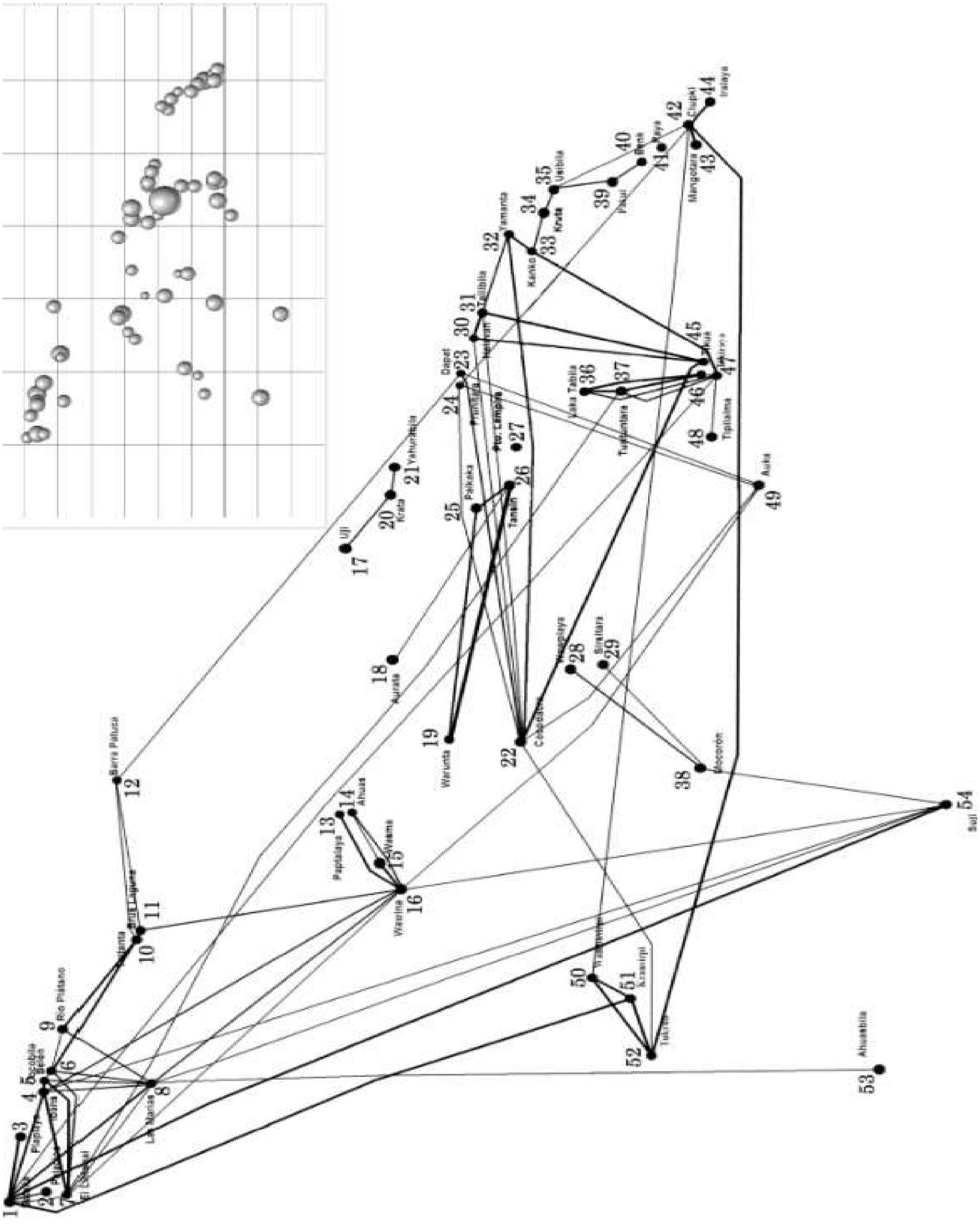

Figure 3 : Isonymyc relations between communities and α values within communities. All values of pairwise isonymy above a value of 0.007 (arbitrarily chosen as threshold) are represented by lines. Line widths are proportional to pairwise isonymy values. Circles in the inserted square represent the communities. The area of a circle is proportional to α value for that community. Bigger circles denote higher surname diversity.

TABLE 5 : Matrix of geographic distances in Kilometers (below diagonal) and Lasker's distances (above diagonal) between pairs of municipalities of the Department of Gracias a Dios, Honduras.

	PL	A	BL	JFB	VM	W
PL	···	2.4895	2.5498	2.5166	2.6098	2.5528
A	63	···	2.3003	2.3631	2.5815	2.3216
BL	99	39	···	2.3124	2.6776	2.4413
JFB	152	90	53	···	2.5902	2.3056
VM	57	121	156	206	···	2.5294
W	90	47	67	99	143	···

Relations between communities inferred from high pairwise isonymy are graphically represented in Figure 3. Although many of these relationships are stronger (wider lines) between geographically closer communities denoting isolation by distance, there are some outstanding exceptions. For instance, the pairs Batalla(1)-Krausirpi(51), Tukrun(52)-Clupki(42) and Batalla(1)-Suji(54) exhibit high isonymy despite of the relative long distances that separate them. Some communities show a relatively abundant number of high relations, as Cocodakra(22), Batalla(1) and Suji(54). Interestingly, Puerto Lempira(27), the most important population in the area, does not show high isonymy relations (i.e. isonymy values between communities above 0.007) with any of the rest of communities. While all isonymy values between Puerto Lempira City and the other communities group in a short, intermediate range (between 0.00163 and 0.00473), all other populations showed at least one extremely low value (i.e. below 0.001).

Figure 4 shows a dendrogram constructed from the matrix of pairwise Lasker's distances between communities using the neighbor joining algorithm as clustering method, as implemented in the *Neighbor* program included in the Phylip software package (freely available in the internet at http://evolution. genetics. washington.edu/phylip/getme.html). As expected, communities strongly tend to cluster within the group corresponding to their respective municipalities.

TABLE 5 shows geographic and Lasker's distance between pairs of municipalities, the former calculated between the capital towns of each municipality. A small (but significant at α level of 0.05) positive lineal correlation between both distances was found, suggesting isolation by distance (Pearson's correlation coefficient of 0.6092, *p*=0.014, 10000 permutations).

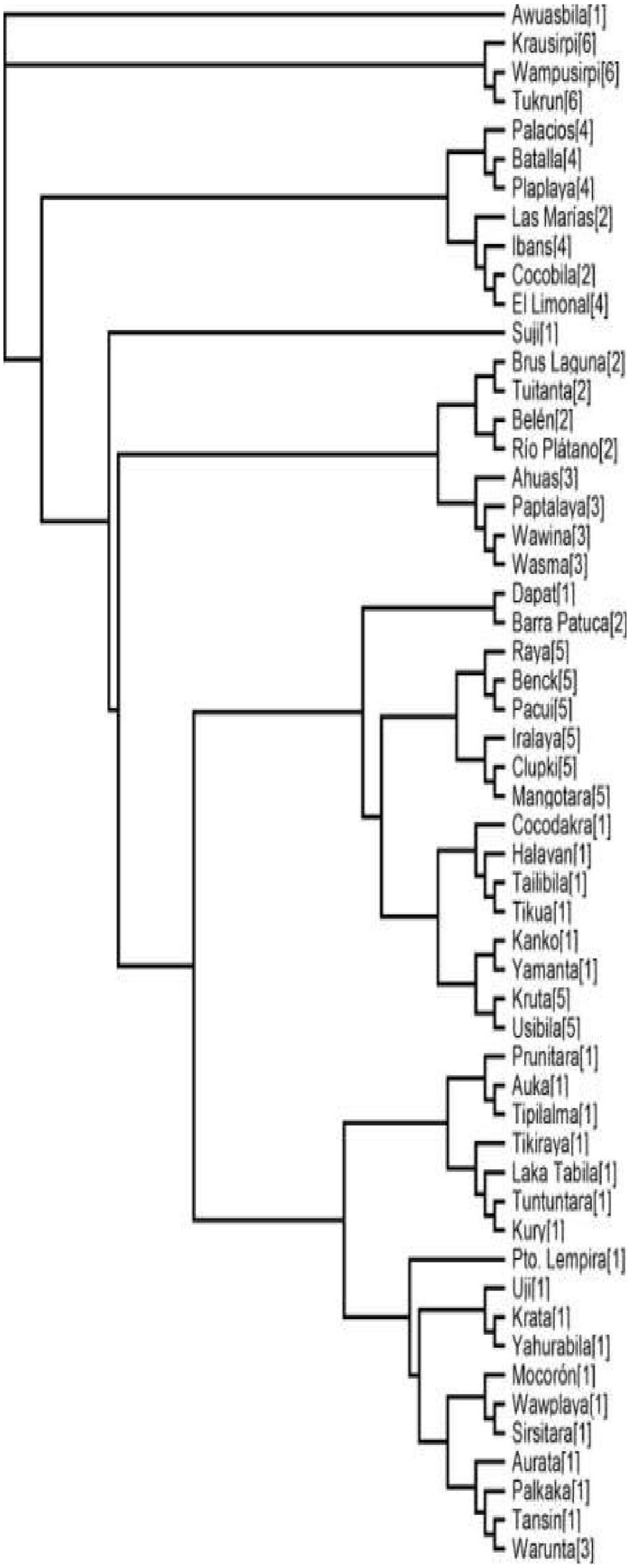

Figure 4 : Dendrogram of Lasker's distances between communities using Neighbor Joining as clustering method. Number inside brackets after each community indicates the department: 1=Puerto Lempira; 2=Brus Laguna; 3=Ahuas; 4=Juan Francisco Bulnes; 5=Villeda Morales; 6=Wampusirpi.

DISCUSSION

There are some considerations related to the characteristics of the sample that could modify F_{ST} values calculated from isonymy that have to be mentioned. For instance, 84 parishes comprise the whole territory of the Honduran Moskitia, but only 54 are represented in the electoral registry. This registry is exhaustive, so, voters of some small communities with only few inhabitants are included in the lists of larger, neighboring communities. Moreover, population structure due to some degree of inbreeding within minor ethnic groups cannot be discarded. These factors may falsely increase surname diversity within communities with the consequent underestimation of F_{ST} values. At the other side, the multiple ethnic origins of the Miskitos and Ladinos should have increased their genetic diversity. In contrast, surnames were transmitted solely by the European fraction and hence, F_{ST} values calculated from isonymy could be overestimated. In other words, surname diversity may not reflect real genetic diversity (increased by admixture), something that has to be taken into consideration when analyzing admixed populations with a unilateral contribution of surnames. Moreover, the existence of gender asymmetries of the proportions of different ethnic contributions in founder populations is the rule in many American populations[36-38].

Additional inherent biases that undermine the assessment of true kinship values are found in the population under study: 1) Polyphyletic origin of surnames. The initial distribution of surnames in the Honduran Moskitia must have been a bottlenecked sample of the distribution in Spain and England during the conquest and colony periods, with the most common surnames overrepresented, and 2) changes due to transcription errors (mutations) where found to be frequent. These biases violate the assumptions for the use of F statistics from the surnames frequencies distribution to assess the exact genetic structure of the population; however, the relatively homogeneous peopling process and history of the region are factors that support an internal consistency that makes this kind of work useful for comparisons among communities, and for the design of future genetic studies.

The availability of two surnames has an advantage for the performance of different calculations. For instance, it may be favorable for the estimation of inbreeding coefficient F_{ST} for the case of autosomal markers. Although Crow & Mange noted that the coefficient is roughly ¼ of random isonymy in sufficiently large samples[21], it can be noted that in populations with different migration customs between both genders, random isonymy calculated solely from first surnames differ from random isonymy from both surnames. In small communities with a strictly patrilocal behavior, historical genetic drift may lower the diversity of Y chromosome markers. In contrast, diversity of autosomal markers could be maintained, or even increased by high female immigrations. In this kind of communities we should observe higher values of random isonymy from first surnames when compared to random isonymy from both surnames. Taking into account the effect of differential migrations over several generations, it is clear that in those cases, the inbreeding coefficient F_{ST} calculated only over first surnames will result overestimated (or underestimated, in matrilocal communities). The use of two surnames would approximate the estimated F_{ST} values (although not fully) to the true values for the case of autosomal markers, and the determination of residence patterns could give us an idea of the effect of gender differential migrations on such values.

Based on observations in populations from Nicaragua, Helms proposed a primarily matrifocal family structure, and therefore, a matrilocal predominance in residence preferences of Miskitos[39]; however, the results presented here suggest that this may not be the case for most of the populations of the Honduran Moskitia. Regarding residence preferences in human groups, two main factors have been postulated: labor division between genders, and warfare (for an extensive analysis and review on this topic, see reference 40). According to Rivas, Miskitos are characterized for living in a continuous struggle for their domains, for which they have become very territorial people[12]. This fact might have, in turn, favored in some extend male phylopatry, nepotism, and a patrifocal family structure, if we assume that fight for land is a task performed preferentially by men. Apparently, belligerence regarding land tenure is common between family groups and with newcomers (mainly Ladinos), despite that most facilities and goods are shared among families within a community.

Patrilocality in most Miskito communities noticeably contrasts with matrilocality in a neighboring population that inhabits the Caribbean coast of Honduras: the Garifuna, which is composed by afro descendant people with strong male migration customs, practices a form of polygyny in which female mates do not share the same house, and holds a strictly matrifocal family structure[16]. In our analysis, the only Municipality in the Department where matrilocality slightly predominates is Juan Francisco Bulnes, not surprisingly the only one with a strong influence from the Garífuna.

Regardless of these findings, residence patterns assessed through isonymy must be taken with caution, and an alternative hypothesis for differential variability of first and second surnames have to be mentioned: male exodus to cities located in other departments, something that could diminish variability of first surnames resembling patrilocality. Flores-Fonseca, using migration matrices, reported very low migration rates in Gracias a Dios, but registered high interdepartmental female migrations in the rest of the country (with the exceptions of departments of Atlántida and Colon, homeland of Garífuna in which male migrations predominate)[41]. In the present study, higher random isonymy for first surnames compared to second surnames (0.00397 and 0.00350, respectively) in the overall department of Gracias a Dios supports male emigration, or alternatively, female immigration from other departments. If the latter is true, patrilocality in Gracias a Dios might be a reflection of high female migration customs in the overall nation. Future studies comparing migration matrices and differential isonymy will be needed to further confirm this.

The same arguments applied to explain higher diversity of second surnames in the department level must stand to explain differences in the community level. High relations between communities would show the most probable migration routes, nevertheless, the nature of these migrations has to be inferred from the obtained values of isonymy between communities analyzed conjunctly with other data. Let us analyze, for example, the pair Warunta(19)-Tansin(26), which showed the higher value of isonymy between communities in this study (0.02264). While Tansin shows a strong matrilocality (58.26%), in Warunta patrilocality predominates (53.47%). Two alternative hypotheses (even though not mutually excluding) could explain this finding: higher male migration from Tansin to Warunta, or higher female migration from Warunta to Tansin in the parents of the electors. In both cases, female diversity would decrease in Tansin and increase in Warunta, and hence, the opposite would occur with male diversity. Again, the information obtain here has to be complemented with analyses performed on migration matrices.

During last century, enormous demographic changes took place in most parts of the world. Streaming of rural residents into large, urban areas (a process referred to as urbanization) originated a transition of metapopulation structure from relatively isolated communities to an outbred structure, with the consequent increase in diversity, which can be revealed through an increased heterozygosity in genetic markers or by a reduction of isonymy[42, 43]. Urbanization might have consequences for health, but also represents a challenge in other areas, as might be in the battle against climate changes and air pollution.

Developing countries in particular, have to be aware of urbanization processes in order to embrace strategies in urban planning, such as the implementation of new technologies in energy, construction, healthcare and crime control on time to buffer potential negative externalities derived from the fast raise in number of inhabitants, and to maximize productivity growth[44, 45]. Particularly, crime control is expected to be difficult in the near future in the Miskito territory, as it is becoming an important part of the cocaine corridor of the Americas, a bridge for drug traffic between South and North America.

In most Honduran territory, large flow of residents from rural to urban centers has been taking place in the last decades[46]; nonetheless, the Department of Gracias a Dios remains mostly rural and isolated from the rest of the country. The City of Puerto Lempira is the only population in Gracias a Dios large enough to be considered in process of urbanization; therefore, some evidence of this process can be obtained from isonymyc data. This evidence include: 1) A very low value for random isonymy within communities when compared to every other location. Moreover, this value is only slightly higher than the values for the overall municipality and the overall department. 2) The high proportion of singletons found in this locality that, regardless of the elevated amount of transcription errors, suggests high recent immigration[47]. 3) The absence of both, low and high isonymyc relations with the rest of the localities, something that could be explained if Puerto Lempira is considered a composition of populations from many other localities due to urbanization. However, it is likely that the prevalent contributions to this city come from nearby communities, as can be inferred from the neighbor joining dendrogram, in which Puerto Lempira City clusters with branches composed mostly by the parishes located in the municipality of Puerto Lempira.

The rest of the Honduran Moskitia, as shown here, is a highly structured population composed mostly of relatively isolated communities. However, the findings in the present work must be complemented with analyses of migration matrices, and with genetic studies from autosomal, mitochondrial, and Y chromosome linked markers to further define the exact nature of differential gender migrations, and to establish admixture estimates and kinship with European, African and American Indigenous populations.

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