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# **Effect of Recent Historical Events on Migration and Isonymic Stratification among the Rama Amerindians from Nicaragua**

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**short title: Migration and Isonymic Estratification among the Rama from Nicaragua**

**Abstract.** The Rama Amerindians from southern Nicaragua are one of few indigenous populations inhabiting the east coast and lowlands of southern Central America. Early 18<sup>th</sup> century ethnohistorical accounts depicted the Rama as a mobile hunter-gatherer and horticulturalists group dispersed in household units along southern Nicaraguan rivers. However, during the 19<sup>th</sup> and 20<sup>th</sup> centuries, Rama settlement patterns changed to aggregated communities due to increased competition for local resources resulting from non-indigenous immigration. This study's objective was to discern the degree of relatedness between and within subdivisions of seven of these communities based on patterns of surname variation and genealogical data. We applied surname analyses (n= 592) to evaluate inter- and intrapopulation variation, consanguinity and substructure estimates and isolation by distance, and used a genealogically based marital migration matrix obtained during fieldwork in 2007 and 2009 to better understand internal migration. Our evaluation indicates a pattern of geographic distribution linking kinships in major subpopulations to nearby family-based villages. Mantel tests provide a correlation ( $r = 0.4$ ;  $P < 0.05$ ) between distance matrices derived from surname and geography among Rama

communities. Genealogical analysis reveals a pattern of kin networks within both peripheral and central populations that is consistent with previous genetic investigations where the Amerindian mitochondrial DNA haplogroup B2 is commonly found among peripheral communities and A2 is frequent in central subpopulations. Marital migration and genealogies provide additional information regarding the influx of non-Ramas to communities near populated villages. These results indicate that the disruption of the Rama's traditional way of life has had significant consequences on their population structure consistent with population fissions and aggregations since the 18<sup>th</sup> century.

The Rama are a Chibchan speaking indigenous population inhabiting the southern Nicaraguan Mosquitia in Central America. Recent demographic surveys indicate fewer than 1500 Rama remain (GTR-K 2007) and no more than fifty individuals are fluent in Rama as a consequence of a linguistic shift to Creole English (Craig et al. 2006). Phylogenetically, this population shares mitochondrial DNA (mtDNA) ancestry with other Chibchan speaking communities from Colombia, Panama, and Costa Rica, demonstrating a high Amerindian component along their maternal line when compared with the degree of European admixture (50%) present in their paternal ancestry (Baldi 2013; Melton et al. 2013).

The first explicit references to a group named Rama appears in ethnohistorical records dating to the 18<sup>th</sup> century, apparently in reference to several distinct groups encountered by Europeans in the lowlands of northern Costa Rica and Southern Nicaragua. Researchers believe that the Rama originated when multiple indigenous populations admixed (Conzemius 1938; Riverstone 2004; Romero 1995); however, it has recently been proposed that a fraction of the Rama population is a remnant of the extinct Voto, a group that inhabited the same area until the

17<sup>th</sup> century. Displaced by European colonization and the Anglo-Spanish war (1761-1763) and held in the San Juan River region between Costa Rica and Nicaragua, a group of Voto relocated to the Punta Gorda River which was inhabited by an earlier Rama group (Baldi 2013).

Ethnohistorical and ethnographic records collected by travelers, merchants, buccaneers, bureaucrats, and ethnographers describe the Rama as a semi-sedentary group dispersed along the rivers and the southern Caribbean coast of Nicaragua (Conzemius 1927; Lehmann 1920; Loveland 1975; Roberts 1978 [1827]; Romero 1996). They subsisted on horticulture, hunting, and fishing, continually moving across their territory in small family units to exploit a variety of microenvironments based on seasonality. Group mobility allowed them to avoid the coast and migrate up river to more interior localities, effectively shielding them from flooding, hurricanes, and the outbreak of infectious diseases associated with climatologic events (GTR-K 2007; Riverstone 2004). As a result of the exploitation of natural rubber, logging, and banana plantations between 1880 and the 1940s by foreign companies, the traditional Rama subsistence pattern was disrupted and an increasing number of Rama families living along the southern Nicaraguan rivers began to relocate to the island of Rama Cay in Bluefield's Bay to avoid epidemics and physical abuse (GTR-K 2007; Mordt 2002; Riverstone 2004). Between the decades of the 1960s and the 1980s, agriculture expansion and the growth of a market economy coupled with an influx of Mestizo migrants from eastern Nicaragua created an increased demand for land and aquatic resources traditionally utilized by the Rama (GTR-K 2007; Loveland 1975; Muller 2001; Riverstone 2004; Schneider 1989).

Despite changes to the traditional Rama subsistence strategy, group mobility, and land access, field researchers from this study (P.M. and N.B.) recently documented domestic networks connecting communities to their home base across many kilometers (Baldi 2013).

Given that these communities are relatively recent phenomena which have not previously been investigated, this study seeks to ascertain the degree of relatedness between and within subdivisions of seven Rama communities based on geographical patterns of surname variation and genealogical data. In order to evaluate surname variation and population subdivisions, it is assumed that the distribution of marital surnames tends to deviate from panmixia due to geographic distance and sociocultural factors. In theory, non-random mating will also have an effect on gene frequencies (Barrai et al. 2002). Deviation from panmixia can be indirectly assessed through the use of methods based on isonymy, or the study and analysis of recurring surnames within a given pedigree (Lasker 1969). Ideally, isonymic models assume that surnames have monophyletic origins and are transmitted from parents to biological children, simulating neutral alleles (Colantonio et al. 2003; Lasker 1991). For this reason, surname distributions can be used for inferring genetic structure, admixture, genetic drift, and estimates of the intensity and directionality of human migrations (Darlu et al. 2012; Koertvelyessy et al. 1988; Lasker 1985; Rodríguez-Larralde et al. 2011). Non-random or assortative mating in human populations can result in surname stratification or subdivision while geographic isolation, conflicts, religion, and other cultural behaviors can contribute to their spatial distribution (Fix 1999; Koertvelyessy et al. 1988; North and Crawford 1996). Isonymic models have been applied to wide ranging studies covering small groups, such as those found in households and villages, to large populations representing entire countries or even continents (Colantonio et al. 2003; Darlu et al. 2012).

The integration of genealogical information with genetic studies has recently been recognized as an important source of information on mutational, cultural, and historical components of human communities which cannot be gleaned from molecular data alone (Larmuseau et al. 2013; Madrigal et al. 2012). In addition to carrying genealogical data,

surnames retain information regarding social and economic conditions relevant to numerous disciplines (Darlu et al. 2012). For example, molecular markers, such as those used to identify mtDNA and the non-combining region of the Y-chromosome (NRY) haplogroups have been employed in determining human population structure and identifying migration patterns. However, these systems cannot detect recent historical events resulting in gene flow over a short period of time. Surname analysis in the context of extended genealogical studies can be used to detect signals of population differentiation during given historical periods and can provide independent and complementary validation of studies based on genomic data (Larmuseau et al. 2013; Pakendorf and Stoneking 2005).

## **Material and Methods**

**The Population.** During intermittent field investigations between 2007-2009, genealogical data were collected from all study participants, as was demographic and ethnographic information from seven Rama communities along the southern Caribbean coast of Nicaragua: Rama Cay, Punta Fría (in Bluefields), Greytown, Punta Águila, Zompopera, Sumu Kat, and Indian River (Figure 1). Distances between these communities were estimated “as the crow flies,” and details of their geographical position is shown in Table 1.

*Rama Cay* is a small island with an area of 0.18 km<sup>2</sup> located in Bluefield’s bay, 15 km south of the village of Bluefields (Loveland 1975). This island, overpopulated since Nicaraguan conflicts during the 1980s, comprises approximately 50% of the Rama population (GTR-K 2007). Moravian missionaries from eastern Germany arrived in 1858 and were influential in cultural changes resulting in the loss or modification of a number of Rama traditions (GTR-K 2007; Loveland 1975; Mueller 1932; Nietschmann and Nietschmann 1974). A chief concern of

the Moravians was the prevention of marriages between Rama and non-Rama individuals, and they enacted behavioral rules to prevent such unions (GTR-K 2007). Since their relocation to Rama Cay, the Moravians kept careful records documenting legitimate and illegitimate unions, deaths, and other demographic events (Moravian-Church 1858-2013). The Rama Cay community subsists on fish of different species, shrimp from nearby rivers (*Macrobrachium sp*) and the coast (*Penaeus sp*), and oysters (*Crassostrea rhyzophora*) gathered in the Bluefield's Lagoon. Cassava, corn, and other crops are cultivated in the adjacent forest; some of these products are sold in Bluefields. A few families from Rama Cay own a second house in the poorest and most depressed neighborhood of *Bluefields*, known as Punta Fría (INIDE 2008).

The community of *Zompopera* is located 12 km west of Rama Cay on the banks of the Kukra River. Prior to its establishment, Rama families inhabiting several of the Kukra's tributaries, now occupied by Mestizos, were amalgamated with the *Zompopera*, who often clash with the Rama over logging, hunting and land invasion (Muller 2001). Increased settlement patterns have exacerbated these hostilities, which has resulted in the accumulation of overlapping households in Sumu Kat and *Zompopera*. *Sumu Kat*, located 40 km west-southwest of Rama Cay via the Kukra River, is inhabited by a community that subsists by fishing the river, planting crops in fields adjacent to their homes, and hunting brocket deer (*Mazama Americana*) and white lipped peccary (*Tayaju pecari*), among others. Surplus resources are sold in the market at the Mestizo town of San Francisco or in Bluefields. Prior to being collectivized by Sandinista policies of the 1980s established to promote new agriculture, the population of Sumu Kat had extended along the Muelle Real, Santa Elena, and Caño Silver river. The influx of Mestizo settlers and foreign land speculators pushed the Rama to less fertile lands (Riverstone 2004; Riverstone 2006) resulting in tense conflicts between the two groups (Schneider 1989).

*Punta Águila*, located 7 km south of Monkey Point, is comprised of only a few houses and a school sitting atop a hill; fishing and turtle hunting are important economic activities due to its proximity to the coast. This village has strong kinship ties with nearby communities of Cane Creek, Punta Gorda, Pastate, Diamante, and Monkey Point. The majority of Rama speakers live in Punta Águila (GTR-K 2007).

*Greytown* (also known as San Juan del Norte) is located near the political border between Costa Rica and Nicaragua. After the Nicaraguan revolution in 1979, numerous Rama families relocated to a Rama neighborhood in this locality. Upriver from Greytown and near the Rio San Juan Wildlife Refuge is the community of *Indian River*, which was re-populated after the Nicaraguan civil war and is comprised of additional communities including La Cucaracha, Canta Gallo and a few scattered hamlets along the river. This area is known for its rich biodiversity and copious rainfall throughout the year.

**Sample and Surname Origin.** Isonymic methods can provide only crude estimates of the intra- and interpopulation variation in small populations when they are subdivided into ethnosocial groups, or if a large number of individuals are from extramarital relationships; however, these difficulties can be minimized if the sample size is large (Colantonio, et al. 2002). In this study, such difficulty was improved by including a large sample size ( $n = 592$  surnames) in relation to the Rama's population size ( $< 1500$  individuals) and its contextualization with other molecular genetic markers, validating the current study.

Using demographic *pro formae*, surnames were collected from participants, along with their spouses, parents, grandparents, and siblings. Surname locations were based on the geographic position of each community (Garmin GPSMAP 60Csx) in order to construct a matrix



based on geography to be compared with those constructed from surnames. All participants in this study gave written informed consent to participate, and approval for study was granted by the Institutional Review Board (IRB# 16735) at the University of Kansas and the Rama community in Nicaragua. Genetic data, including mtDNA and NRY data from this population have previously been reported (Baldi 2013; Melton et al. 2013; Melton 2008).

According to historical records, Rama Amerindians inherited their current surnames from British buccaneers and Creole merchants who resided on the Caribbean coast during the 18th century, while the Moravian missionaries established the rules of surname transmission in an effort to ensure monogamous relationships among native communities (Moravian-Church 1858-2013). In the ecclesiastical records at Rama Cay, individuals conceived through illegitimate unions were given only their mother's surname (GTR-K 2007). Historically, most Rama families had British surnames but Spanish and Creole surnames have become frequent more recently due to Mestizo admixture (GTR-K 2007).

Rama surname transmission follows the Iberoamerican surname system (IASS) in which every individual inherits two surnames, the first surname is that of his or her father, and the second surname is from his or her mother (Pinto-Cisneras et al. 1985). Verification of this system among the Rama was achieved through genealogical reconstructions. Because surnames are inherited paternally among all members of the Rama, the surnames of female participants were included in the sample in order to model both lines of descent as marked by surname inheritance and to augment the sample size (Lasker 1985).

**Analytic Procedures.** Based on demographic information gathered in the field, genealogies were reconstructed using GenePro v.2.0.0.2. Genograms generated through this program

establish the genetic identity between individuals and communities as well as eliminating duplicate records and combining surnames with similar spellings as is typical in isonymy studies. Statistical calculations were performed using the programming language R (R Development Core Team 2011) with the biodemographic package Biodem (Boattini et al.2012), as well as in Microsoft Excel, which yielded equivalent results. Non-metric multidimensional scaling plots (MDS) were constructed in order to visualize synthetic relationships between Rama communities with NTSYS v.2.21 (Rohlf 2002).

A migration matrix was constructed from genealogical information to demonstrate marital migration and network relationships between Rama communities. Each element of the matrix,  $m_{ij}$ , provides the probability that an individual in population  $j$  came from population  $i$ . Once computed, these elements were standardized by dividing corresponding column totals (Relethford 2012).

In order to determine within population variation for each community, four test statistics were calculated: Unbiased random isonymy ( $I_{ii}$ ), Fisher's alpha ( $\alpha$ ), Lasker's coefficient of isonymy within populations ( $R_i$ ), and the kinship parameter phi ( $\Phi_{ii}$ ). Unbiased random isonymy  $I_{ii}$  (Relethford 1988) approximates the amount of isolation existing in subpopulations. High values indicate an elevated degree of isolation and low values suggest increased migration and resulting admixture (Rodríguez-Larralde 1993). Morton's *a-priori* kinship  $\Phi_{ii}$ , described by Relethford (1988), identifies values of kinship within populations. Fisher's  $\alpha$  (Fisher 1943) was used to estimate surname diversity and to infer genetic isolation which is analogous to the effective number of alleles in a genetic system. Large Fishers'  $\alpha$  values suggest higher migration rates while low levels indicate isolation, increased consanguinity, and genetic drift (Bronberg et

al. 2009). Lasker's  $R_i$  (Lasker 1985) provides an estimate of surname relationships within communities.

The relationship between Rama subpopulations was explored, by applying the following test statistics: Lasker's coefficient of relationship ( $R_{ib}$ ), Isonymy coefficients ( $I_{ij}$ ), and kinship between subpopulations ( $\Phi_{ij}$ ). Lasker's  $R_{ib}$  evaluates the degree of surname affinity, assuming that individuals with a common surname are more closely related than those without such similarities (Colantonio et al. 2003). Lasker's  $R_{ib}$  has previously been defined between pair populations (Sanna et al. 2006). A matrix of random isonymic values  $I_{ij}$  illustrated surname affinity between subpopulations.  $I_{ij}/4$  has previously been described by Relethford (1988) as values of an *a-priori* kinship matrix between populations  $\Phi_{ij}$ .

Population subdivision was investigated with the repeated-pairs ( $RP$ ) approach that approximates population substructure, or the degree of subdivision of a population occurring in subgroups that reproduce, by following the lineage-like behaviors of mate selection. If two populations have different allele frequencies, the overall heterozygosity is reduced causing population subdivisions or population substructure which can result from geographic barriers to gene flow (genetic drift) and/or other culturally associated behaviors of preferential mating systems. The resulting impact on gene frequencies is known as the *Wahlund effect*, which is defined as a reduction of heterozygosity in a population caused by subpopulation structure (Koertvelyessy et al. 1988). This statistic is calculated by the formula:

$$RP = \frac{\sum [s_{ij}(s_{ij} - 1)]}{N(N-1)} \quad (1),$$

where  $S_{ij}$  is the number of marriages with a husband of the  $i$ th surname and a wife of the  $j$ th surname, and  $N = \sum S_{ij}$ . In order to determine the amount of repetition expected at random, the surnames of wives and husbands were rearranged in random order ( $RP_r$ ) using a model proposed by Chakraborty (1985).  $RP$  scores reveal preferential interlineage marriage patterns (avoidance or close inbreeding). If frequencies differ between preferred and non-preferred surnames, any repeated mate preference will elevate  $RP$  values above randomly expected levels; in other words, an excess of  $RP$  on  $RP_r$ , calculated as  $(RP/RP_r)/ RP_r$  will suggest a degree of subdivision internal to a subpopulation (Lasker and Kaplan 1985).

Deviations from panmixia were estimated using Crow's method, which includes three components ( $F_t$ ,  $F_r$ , and  $F_n$ ) (Crow 1980; Crow and Mange 1965). Inbreeding coefficients relative to total population are expressed by  $F_t$ . The random component  $F_r$  measures departures from panmixia within a descendant population which is averaged over all subpopulations. This value is dependent on population size, where a smaller population has a higher probability of marital couples sharing the same surname (González-Martin et al. 2006). Any divergence of a descendant population from a founder population is measured by the nonrandom component  $F_n$ . This value represents the deviation between  $F_t$  and  $F_r$ . Positive values designate preference between consanguineous marriages, and negative values demonstrate a tendency to avoid marriages with partners who share a surname. This relationship is described as:

$$F_t = F_n + (1 - F_n) * F_r \quad (2),$$

with the random component expressed as:

$$Fr = \sum(p_i * q_i) / 4 \quad (3),$$

where  $p_i$  is the frequency of surname  $i$  in paternal surnames, and  $q_i$  is the frequency of surname  $i$  in maternal surnames. The nonrandom component is calculated with the formula:

$$F_n = \frac{(P - \sum p_i * q_i)}{4 * (1 - \sum p_i * q_i)} \quad (4),$$

where  $P$  is the frequency of marriages with isonymic surnames.

In the context of these analyses ( $RP$  and  $F$ -statistics), high inbreeding does not necessarily suggest a resulting preference for consanguineous marriages but may instead indicate that an overall lack of mate choices has resulted in an increase of marital unions between individuals sharing a surname (Relethford 2012).

Isonymy distances between the seven Rama communities were estimated using Lasker's distances  $D$  (Rodríguez-Larralde et al. 1998) and Euclidian distances  $\theta$  (Cavalli-Sforza and Edwards 1967). Geographic distances were measured "as the crow flies," using the GPS coordinates for each community. Isonymy and geographical distance matrices and Lasker's  $R_{ib}$  matrices were compared using Mantel's tests (Mantel 1967).

## Results

**Surname Distribution.** The five most frequent surnames among Rama communities were Macrea (23%), Ruiz (6%), Daniel (6%), Hodgson (6%), and Martínez (5%). Additional Spanish or Creole surnames were observed at low in frequency in all communities (between 1% and 4%). These results were consistent with kinship networks between communities based on genograms

(not shown), where frequent surnames among communities have more intra- and intercommunity familial links. Genealogies in which surnames associated with Spanish and Creole origin have fewer familial linkage relationships between communities.

**Marital Migration and Mate Choice.** Table 1 provides geographic information and distances between Rama Cay and the other communities investigated. Approximately 94% of the individuals in the sample were born within Rama territory, and the remaining individuals were either non-Ramas who married an individual of Rama descent or non-Rama immigrants. Moreover, married individuals born within Rama territory were found to have traveled as far as 100 kilometers when relocating to other Rama communities.

The majority of participants were born in Rama Cay prior to migrating off the island (> 47%). Approximately 91% of participants born in Rama Cay remained in the village while 20% remained in Punta Águila, and 7-15% retention was observed in Sumu Kat, Zompopera, and Bluefields. No participants from Greytown or Indian River were born within their residential community. Fewer than 5% of participants born outside Rama territory in locations such as Managua and Limón, Costa Rica, resided in Punta Águila, Greytown, Indian River, and Rama Cay. Punta Águila had the greatest number of individuals born in another Rama village such as Cane Creek, Torsuani River, Red Bank, and Wiring Cay (Table 2).

**Intra Population Variation.** Among intrapopulation statistics (Table 3) unbiased isonymy  $I_{ii}$  infers that Bluefields, Indian River and Sumu Kat are the most isolated communities when compared with Rama Cay, Punta Águila, while Greytown and Zompopera have intermediate values. Low isonymy values indicate that Rama Cay, Punta Águila, and Greytown have a greater

diversity of mate choice based on surname data. Fisher's  $\alpha$ , similar to  $I_{ii}$ , measures genetic isolation and can be used to estimate migration. High Fisher's  $\alpha$  values were found in Greytown, Punta Águila, Rama Cay, and Zompopera, indicating gene flow. On the contrary, Bluefields, Indian River, and Sumu Kat appear to be the most isolated communities. Kinship values within populations  $\Phi_{ii}$  and Lasker's  $R_i$  correspond with these findings, which is illustrated by higher values in Sumu Kat, Bluefields, and Indian River, contrasting with the lower values found in Greytown, Rama Cay, Punta Águila, and Zompopera. Higher kinship values suggest communities are more isolated and have been affected less by gene flow. These findings demonstrate that Sumu Kat, Bluefields, and Indian River are represented by higher kinship values and greater isolation while a second group (Greytown, Rama Cay, Punta Águila, and Zompopera) is less isolated and has had more immigration.

**Inter Population Variation.** Surname variation within populations is shown in the MDS plot in Figure 2. This plot depicts a cluster of exogamous populations (Greytown, Zompopera, Rama Cay, and Punta Águila) based on Lasker's  $R_{ib}$ . Within this group, Greytown is the most admixed community. In contrast, Bluefields, Sumu Kat, and Indian River are more endogamous. This interpretation is concordant with  $Fr$  and  $RP$  values shown in parenthesis.

Lasker's  $R_{ib}$  (Table. 4) indicates that the majority of communities are correlated ( $\geq 0.05$ ) with at least one other community. For example, Rama Cay is highly correlated with Greytown, and Greytown correlates with four other communities (Sumu Kat, Indian River, Zompopera, and Bluefields) while Punta Águila differs from a general pattern of communal correlation, having less surname affinity with the other six Rama communities.

The coefficient of kinship,  $\Phi_{ij}$ , measures loss of heterozygosity between populations as a function of geographic distance (Relethford 1988). MDS plots based on  $\Phi_{ij}$  (not shown) and unbiased random isonymy  $I_{ij}$  (Figure 3) had comparable results. Rama Cay, Punta Águila, Greytown, and Zompopera were the most heterozygous communities as evidenced by their marginalized locations in the corners of the plot. Indian River, Bluefields, and Sumu Kat were close to the centroid of the plot, illustrating homozygosity. Unbiased isonymy values  $I_{ii}$  are included in parenthesis and show corresponding spatial relationships with  $I_{ij}$  values.

**Biodemographic Structure.** Inbreeding levels for Rama Amerindians derived from the Crow components ( $F_t$ ,  $F_n$ , and  $F_r$ ) are summarized in Table 5. Zompopera and Sumu Kat have the highest value of total consanguinity ( $F_t$ ), while Punta Águila and Rama Cay are intermediate in comparison to Greytown, Bluefields, and Indian River. The random component of inbreeding ( $F_r$ ), equivalent to  $F_{st}$ , resulted in higher values for the smallest and most isolated populations (Sumu Kat, Indian River, Bluefields, and Zompopera) while Punta Águila, Rama Cay, and Greytown are less influenced by drift. The non-random component ( $F_n$ ) indicates that all populations except for Zompopera show aversion towards unions between consanguineous mates due to their negative values.

The highest proportions of surname repeats  $RP$  (Table 5) are found in Bluefields, Indian River, and Sumu Kat while lower values were found in Greytown, Rama Cay, Punta Águila, and Zompopera. Ratios of  $RP$  on  $RP_r$ , calculated as a percentage, show population substructure in decremental order of subdivision: Punta Águila, Greytown, Bluefields, Indian River, and Zompopera. Of these, Punta Águila and Greytown have the highest degree of subdivision or



population substructure while Rama Cay and Sumu Kat were characterized by less internal substructure or intergroup subdivisions.

**Isolation by Distance.** Lasker's  $D$ , Euclidian  $\theta$ , and Lasker's  $R_{ib}$  (Table 6) were used to evaluate isolation by distance based on surnames and evaluated against geographic distances between seven Rama villages: Each distance matrix was found to be significantly correlated with a matrix based on geography. Results of these mantel tests were as follows: Euclidian  $\theta$  ( $r = 0.42, p = 0.03$ ); Lasker's  $D$  ( $r = 0.43, p = 0.05$ ). Euclidian  $\theta$  were found to weakly correlated with Lasker's  $R_{ib}$  ( $r = 0.26, p = 0.04$ ).

Lasker's  $R_{ib}$  and geographic distances were not significantly correlated ( $r = 0.26, p = 0.08$ ) and the additional matrices (Lasker's  $D$  with Euclidian  $\theta$ , and Lasker's  $D$  with Lasker's  $R_{ib}$  resulted in negative associations) had borderline significant correlations. Lasker's  $D$  depicts the geographic relationships between Rama communities (Figure 4) based on surname distances in multidimensional space. This plot resulted in clusters between Bluefields, Sumu Kat, Zompopera, and Rama Cay as well as one between Greytown and Indian River while Punta Águila was more isolated. These relationships are concordant with the geographic dispersion of these communities.

## **Discussion**

Mantel tests comparing distance matrices (Lasker's  $D$ , Euclidian, and geographic) resulted in significant correlations between geography and surname distributions, demonstrating that kinship decreases exponentially with distance as predicted by Malecot's isolation by distance model (Dipierri et al. 2005). This suggests that individuals who share the same surname, and are thus

theoretically related biologically, are not randomly distributed in geographical space. However, communities are not totally isolated from each other and they are interconnected by complex networks that serve to maintain familial and social relationships across the territory. For example, Rama Cay serves as the major “population hub” where a great number of individuals are born, marry, and leave after establishing a family. This phenomenon is known as kin-structured migration (KSM), or a type of migratory behavior in which fragmentation, movement, and relocation occur among populations of high mobility such as hunter-gathers and mobile horticulturalists. In KSM, the unit of migration is the familial group and not the individual (Fix 1999). As documented among the Rama by Loveland (1975), KSM families typically relocated to communities where other relatives have already settled (satellite communities), although the connection with the parental community (in this case, Rama Cay), is not lost and families and individuals generally return for holidays, funerals, or to visit the local clinic, as observed during fieldwork. Punta Águila is an exception to this rule because a number of individuals born within the community or adjacent communities (Cane Creek, Torsuani River, Red Bank, and Wiring Cay) remain located in the vicinity (see Table 2). Isonymy results were consistent, illustrating patterns of regional migration based on marital ratios and genealogies between communities. This is exemplified by Lasker’s  $R_{ib}$  that suggests that communities are differentially connected through kinship to residential units of small population size (satellite populations). Two main kinship networks emerge from between populations correlations (Figure 5), one between the main peripheral communities (Rama Cay and Greytown) with satellite populations including Sumu Kat, Zompopera, Indian River and Bluefields ( $R_{ib}$ : 0.05–0.09), and another between Punta Águila (central population) and Bluefields ( $R_{ib}$ : 0.05). These results describe likely gene flow events occurring between these two networks.

As a summary, surname analyses describe Rama groups subdivision into two groups of communities related by strong kin ties. The first group includes a network between communities in the peripheral area of the Rama territory including Rama Cay, Greytown, Zompopera, Sumu Kat, Indian River, and Bluefields (Punta Fría) and the second group includes a network between Punta Águila Cane Creek, Torsuani River, Red Bank, and Wiring Cay. These last populations are located north of the Punta Gorda River and can be considered “central populations”.

As an independent test of the genetic differentiation between central and peripheral populations Baldi (2013) performed analysis of molecular variance (AMOVA) (Excoffier et al. 1992) and the Monmonier algorithm (Monmonier 1973) on mtDNA HVS-I sequences in order to detect barriers of gene flow and genetic segregation. According to AMOVA results, 9.5% of variation is explained among peripheral and central groups ( $F_{ct} = 0.09$ ,  $P < 0.001$ ) while 87.2% ( $F_{st} = 0.13$ ,  $P < 0.001$ ) of the total genetic variation is explained within Rama communities. Congruent with AMOVA, the Monmonier algorithm found a strong genetic barrier of gene flow separating Punta Águila from the remaining five Rama communities. Geographically, this barrier is estimated to be between the Bluefields Lagoon and Punta Gorda River. Marital practices, probably based on assortative mating within groups, created the consanguineal relationships and alliances that underlie the genetic structure of the Rama and may be maintained for generations, explaining the observed division between central or peripheral communities. This might explain the high incidence of the mtDNA haplogroup A2 in Punta Águila as opposed to haplogroup B2 among the communities in the peripheral group (Baldi 2013).

Surname diversity corresponds with the degree of isolation calculated with unbiased isonymy  $I_{ii}$ , Fisher's  $\alpha$ , kinship relationships  $\Phi_{ii}$ , and Lasker's coefficient of relationship within populations  $R_i$ . In general, the most populated communities (Greytown, Rama Cay, and Punta

Águila) are less isolated and receive the largest migratory influx of non-Rama males and Zompopera is somewhat intermediate. Furthermore, the most geographically and biologically isolated populations are Sumu Kat and Indian River. These communities can only be accessed by river, which requires two days of traveling by canoe or approximately ten hours in a motor boat. The Rama neighborhood (Punta Fría) in Bluefields appears to be genetically isolated; however, the sample size was small and statistically limited.

Inbreeding estimates ( $F$ -statistics), and the detection of population substructure ( $RP$ ) present additional aspects of Rama mating structures that are complementary with each other, and help evaluate sampling errors caused by small sample sizes (North and Crawford 1996).  $F_r$ , or the random component of inbreeding, analogous to  $F_{st}$ , estimates the amount of inbreeding expected by chance within each community. In populations such as Indian River, Sumu Kat, Bluefields, and Zompopera the probability (values between 0.0236 and 0.0679, in Table 4) that prospective mates are closely related was higher because there are smaller pools of potential non-related mates when compared to Punta Águila, Rama Cay, and Greytown. The  $F_n$  component of consanguinity indicates that Zompopera has the highest incidence of unions between individuals who share a common surname (Blayat, Ruiz, and Macrea account for 51% of surnames). Additionally, Zompopera has the highest rate of individuals who were born and stayed in the community. The repeated-pair approach illustrates Punta Águila and Greytown as being the most internally subdivided communities, as opposed to Rama Cay and Sumu Kat, which show less aversion toward interlineage marriages. Zompopera which had a near-negative value, may have similar behavioral patterns.

Although the Rama kinship system has historically been endogamous, exogamous marriages with Mestizos have gained in frequency during the last two generations. Exogamous

marriages have occurred between Rama, Miskitu, and Mayagna (Sumu) groups for two centuries and with Creoles during the past few decades (GTR-K 2007). According to census data (2005-2007) carried out by the regional government, of 88 mixed unions recorded in five Rama communities, 60% of these exogamous unions occurred between Rama women and Mestizo men, 24% between Rama and Miskito, and 16% between Rama and Creole. The majority of these unions occurred in Rama Cay, Greytown, and Punta Águila (GTR-K 2007). In concordance with surname analyses the degree of exogamous marriages among the most populated Rama communities is relative to their proximity to Mestizo and Creole communities and to increased immigration rates from the Pacific coast of Nicaragua during the second half of the 20th century. This might explain the high incidence of European NRY haplogroups R1b1b2 and G2a2 (50%), coupled with 50% Native American haplogroup Q1a3a among males inhabiting Sumu Kat and Rama Cay (Melton et al. 2013).

Additional information on molecular genetic diversity (Baldi 2013) was provided by two mtDNA parameters: the number of variant sites between genetic sequences ( $\theta_s$ ), and nucleotide diversity ( $\theta\pi$ ) show that Rama Cay and Greytown have the highest maternal genetic diversity compared to Zompopera, Indian River, Sumu Kat, and Punta Águila. In addition, of the 17 haplotypes found in the Rama population, 12 were reported in Rama Cay, 6 were found in Greytown, and 6 in Punta Águila. Most of these mtDNA haplotypes are associated with the haplogroups A2 (28%) and B2 (71%), although two individuals share the Amerindian haplogroup C1 and the African L3 (1%). The last mtDNA haplogroup is a signature of recent African admixture in the community of Greytown. It may be noted that surname and diversity parameters based on mtDNA provided a fairly concordant estimation of the isolation and gene diversity expected among different Rama communities.

In conclusion, surname analysis and genealogical reconstructions provide information regarding the effect an influx of non-Rama migrants has had on the population structure of seven Rama communities, and that a pattern of kinship networks exists between peripheral populations and central populations within the Rama territory. Immigration occurring in the Rama territory was a major cause of community aggregations and has had a significant impact on Rama dispersions which were traditionally exhibited by separated households arranged along rivers and tributaries in the lowlands of southern Nicaragua (GTR-K 2007; Loveland 1975; Romero 1995; Schneider 1989). This phenomenon has been more pronounced since the mid-20<sup>th</sup> century with the expansion of agriculture by waves of migrants from the Pacific coast of Nicaragua (GTR-K 2007; Riverstone 2004). Consequently, gene flow is more frequent between immigrant males of non-Rama origin with Rama women in those communities that are in close proximity to populated towns such as Bluefields and Greytown, and in Punta Águila due to its proximity to Monkey Point and the frontier of colonization. Additionally, these results indicate the existence of a pattern of kin networks within both peripheral populations and central populations. The peripheral group might correspond to the Voto-Rama Amerindians that migrated north after their fission from to the San Juan River in the 18<sup>th</sup> century, and later moved to the Bluefield's Bay and adjoining rivers. The existence of a central Rama group inhabiting the Punta Gorda River region first appeared in ethnohistorical references from the 18<sup>th</sup> and 19<sup>th</sup> centuries. This group has been partially isolated from the peripheral group (Riverstone 2004). The migration and partial isolation of both groups is consistent with the myths of creation and migrations recompiled by Loveland (1975) and their genetic subdivision (Baldi 2013).

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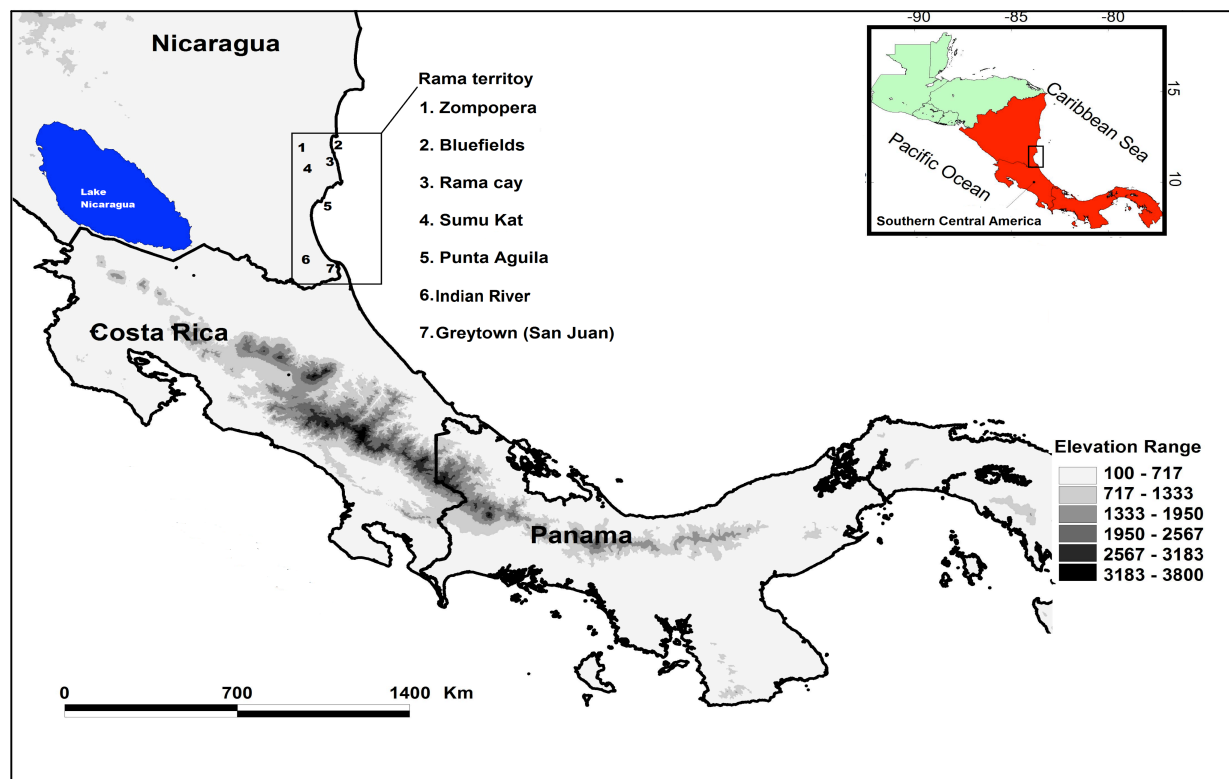


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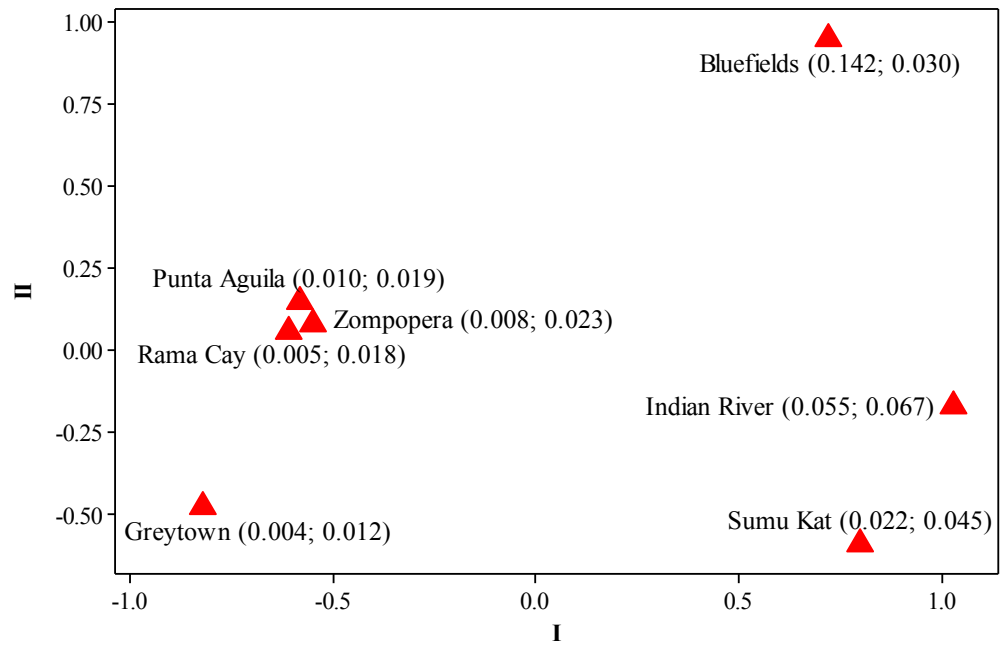
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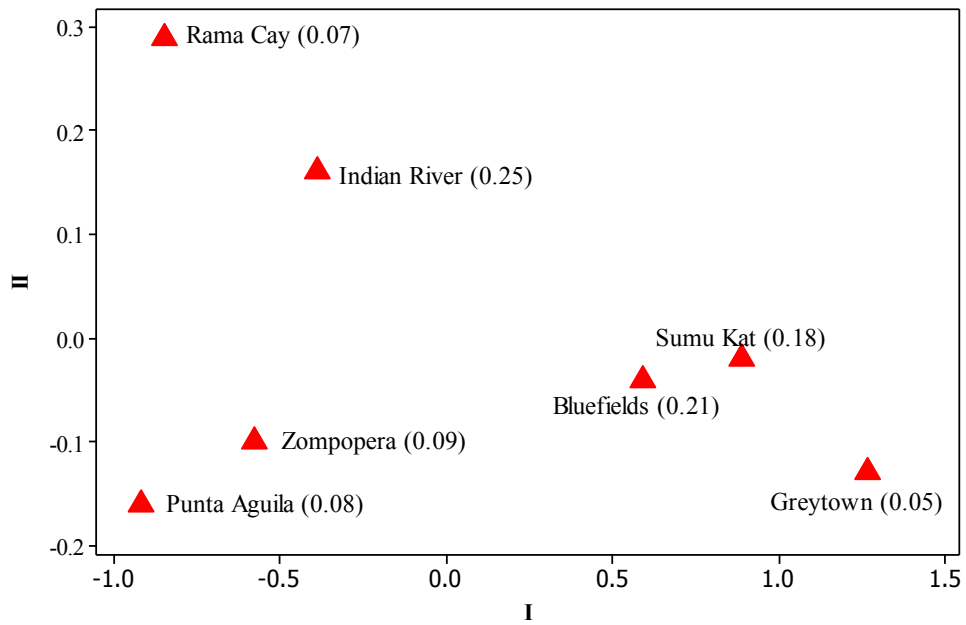


**Figure 1.** Rama territory and seven localities visited during fieldwork in the southern Caribbean region of Nicaragua (Baldi 2013).



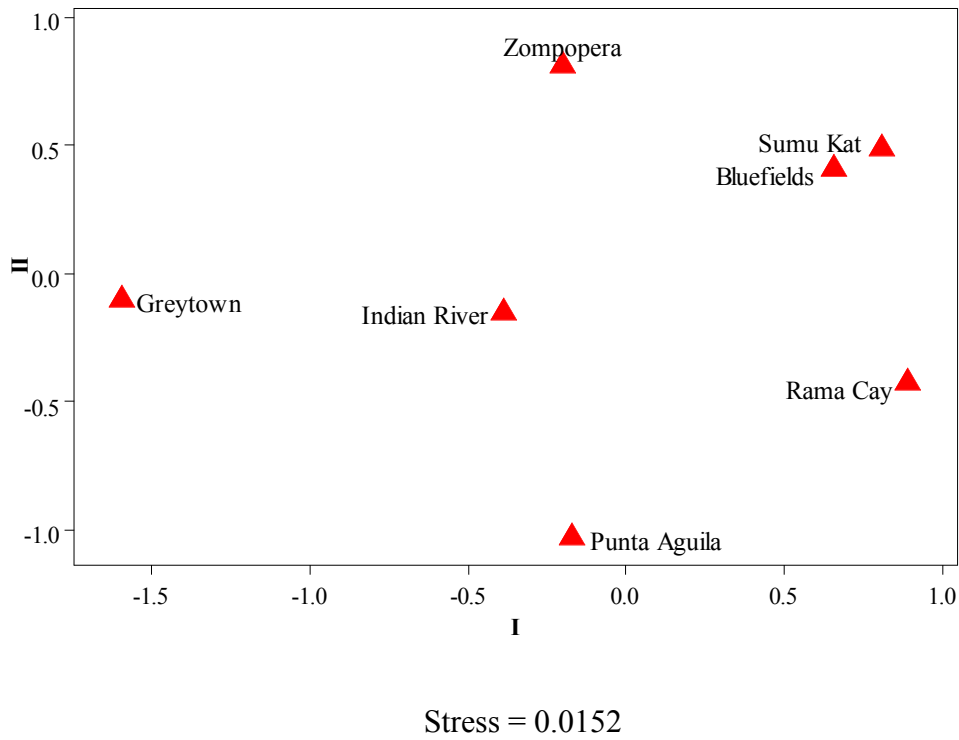
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**Figure 2.** MDS of Lasker's  $R_{ib}$  values showing, exogamous communities (clustered in left side of plot) and endogamous populations (clustered in right side of plot).  $RP$  and the  $F_r$  values, e listed in parenthesis.

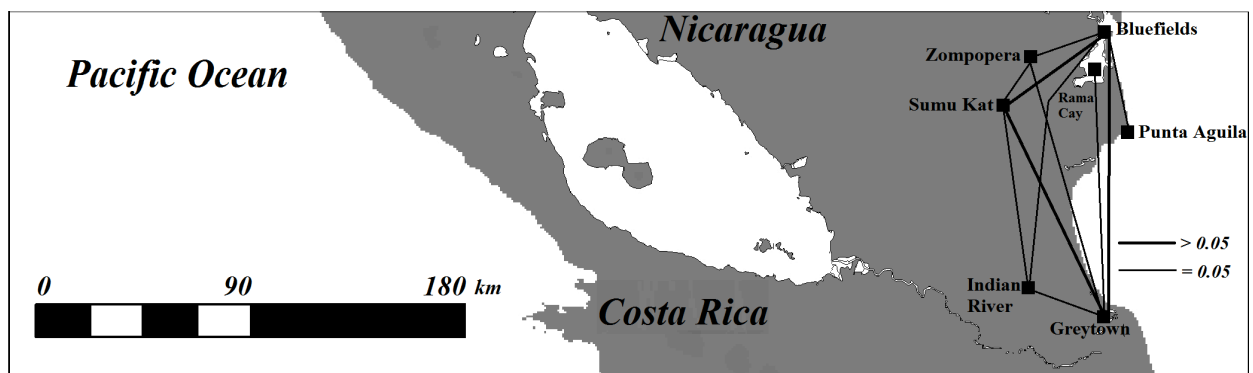


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**Figure 3.** MDS of Isonymy coefficients between communities ( $I_{ij}$ ) and unbiased isonymy values in parenthesis ( $I_{ii}$ ). Exogamous populations are outliers (Greytown, Punta Águila, Zompopera, and Rama Cay), whereas endogamous populations are closer to the centroid (Bluefields, Sumu Kat, and Indian River).



**Figure 4.** MDS of Lasker's  $D$  showing kinship relationships based on isonymy between populations. Lasker's  $D$  correlates with the geographical position of the communities.



**Figure 5.** Map of Lasker's  $R_{ib}$  showing major surname associations between seven Rama communities. Lower values than 0.05 are omitted.



**Table 1.** Geographic positions and marital distances of seven Rama communities. Distances are measured in straight lines.

Rama subpopulation	Geographic Coordinates (N-W)	Distance from Rama Cay (km)	Both partners were born in the Rama territory (%)	At least one partner was born outside the Rama territory (%)
Sumu Kat	11 47 21.21- 84 3 42. 81	29.5	94.7	5.3
Bluefields	12 0 23.47- 83 45 43.48	14.6	100	0
Punta Águila	11 34.240 - 83 43.326	35.6	93.1	6.9
Greytown	10 56.701- 83 43.917	103.9	93.6	6.4
Indian River	11 06.148- 83 54.206	86.6	94.7	5.3
Zompopera	11 53.705- 83 56.114	13.9	84.6	15.4
Rama Cay	11 52.926- 83 48.493	0	96.2	3.8

**Table 2.** Migration Matrix for Rama subpopulations.

Community of Origin ( <i>i</i> )	Community of residence ( <i>j</i> )						
	Punta Águila	Greytown	Indian River	Rama Cay	Sumu Kat	Bluefields	Zompopera
Punta Águila	0.2045						
Greytown			0.0135		0.0053	0.0323	
Indian River				0.0053			
Rama Cay	0.4773	0.7297	0.8095	0.9101	0.7903	0.9231	0.7458
Sumu Kat	0.0227			0.0053	0.1290		0.0678
Bluefields	0.1364	0.1622	0.0526	0.0529	0.0323	0.0769	0.0169
Zompopera		0.0135		0.0053			0.1525
Other Rama villag.	0.1136	0.0270		0.0106			
No Rama villag.	0.0455	0.0541	0.0526	0.0053			

**Table 3.** Isonymy analysis of seven Rama localities: The sample size is denoted by N and S is the number of surnames in each community.

Subpopulation	N	S	$I_{ii}$	$\alpha$	$R_i$	$\Phi_{ii}$
Greytown	136	31	0.050000	20.00000000	0.028493	0.012500
Rama Cay	204	33	0.073698	13.56880734	0.039120	0.018425
Punta Águila	62	14	0.080910	12.35947712	0.047867	0.020227
Zompopera	82	18	0.094851	10.54285714	0.052945	0.023713

Sumu Kat	76	19	0.189123	5.287569573	0.099896	0.047281
Bluefields	14	4	0.208791	4.789473684	0.132653	0.052198
Indian River	18	3	0.248366	4.026315789	0.145062	0.062092

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**Table 4.** Matrix of Lasker's coefficient of relationship between communities ( $R_{ib}$ ). The highest correlations between communities are shown in bold.

Subpopulation	Bluefields	Rama Cay	Greytown	Punta Águila	Zompopera	Sumu Kat	Indian River
Bluefields	1.0000						
Rama Cay	0.0399	1.0000					
Greytown	<b>0.0794</b>	<b>0.0519</b>	1.0000				
Punta Águila	<b>0.0541</b>	0.0216	0.0394	1.0000			
Zompopera	<b>0.0537</b>	0.0266	<b>0.0547</b>	0.0317	1.00000		
Sumu Kat	<b>0.0865</b>	0.0405	<b>0.0980</b>	0.0416	<b>0.05044</b>	1.00000	
Indian River	<b>0.0575</b>	0.0258	<b>0.0528</b>	0.0242	0.03464	<b>0.05608</b>	1.00000

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**Table 5.** Inbreeding coefficients and values of population subdivision among seven Rama localities.

**Table 6.** Mantel correlations between distance matrices and Lasker's  $R_{ib}$  coefficients. Significant p-values ( $p < 0.05$ ) are in bold and above the diagonal while  $r$  values are listed below the diagonal.

Subpopulation	$Ft$	$Fr$	$Fn$	$RP$	$RP_r$	% difference
Greytown	-0.00049	0.012435	-0.01309	0.004829	0.002501	0.930806
Bluefields	-0.00320	0.030612	-0.03488	0.142857	0.095238	0.500000
Indian River	-0.01899	0.067901	-0.09322	0.055556	0.042438	0.309091
Punta Águila	0.007311	0.019771	-0.01271	0.010753	0.005272	1.039474
Rama Cay	0.009278	0.018551	-0.00945	0.005048	0.005342	-0.05506
Sumu Kat	0.023236	0.045014	-0.02280	0.022760	0.032687	-0.30370
Zompopera	0.044174	0.023647	0.021025	0.008537	0.008043	0.061391

	Geography	Lasker 's $D$	Euclidian $\theta$	Lasker's $R_{ib}$
Geography	1	<b>0.05</b>	<b>0.03</b>	0.08
Lasker's $D$	<b>0.43</b>	1	0.55	0.54
Euclidian $\theta$	<b>0.42</b>	-0.02	1	<b>0.04</b>
Lasker's $R_{ib}$	0.26	-0.05	<b>0.43</b>	1