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RESEARCH ARTICLE

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Residence rule flexibility and descent groups dynamics shape uniparental genetic diversities in South East Asia

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Abstract

Objectives: Social organization plays a major role in shaping human population genetic diversity. In particular, matrilocal populations tend to exhibit less mitochondrial diversity than patrilocal populations, and the other way around for Y chromosome diversity. However, several studies have not replicated such findings. The objective of this study is to understand the reasons for such inconsistencies and further evaluate the influence of social organization on genetic diversity.

Materials and Methods: We explored uniparental diversity patterns using mitochondrial HV1 sequences and 17 Y-linked short tandem repeats (STRs) in 12 populations ($n = 619$) from mainland South–East Asia exhibiting a wide range of social organizations, along with quantitative ethno-demographic information sampled at the individual level.

Results: MtDNA diversity was lower in matrilocal than in multilocal and patrilocal populations while Y chromosome diversity was similar among these social organizations. The reasons for such asymmetry at the genetic level were understood by quantifying sex-specific migration rates from our ethno-demographic data: while female migration rates varied between social organizations, male migration rates did not. This unexpected lack of difference in male migrations resulted from a higher flexibility in residence rule in patrilocal than in matrilocal populations. In addition, our data suggested an impact of clan fission process on uniparental genetic patterns.

Conclusions: The observed lack of signature of patrilocality on Y chromosome patterns might be attributed to the higher residence flexibility in the studied patrilocal populations, thus providing a potential explanation for the apparent discrepancies between social and genetic structures. Altogether, this study highlights the need to quantify the actual residence and descent patterns to fit social to genetic structures.

KEYWORDS
kinship system, mitochondrial DNA, Y chromosome, matrilocal, patrilocal

1 | INTRODUCTION

Larger worldwide genetic differences between human populations have been reported for Y chromosome than for mitochondrial DNA (Lippold et al., 2014; Seielstad et al., 1998; Wilkins and Marlowe, 2006). This pattern has been mainly attributed to the high prevalence of patrilocality, with 70% of human populations thought to be patrilocal (Godelier, 2004; Levinson and Malone, 1980; Marlowe, 2000). Indeed patrilocality, which is a type of postmarital residence in which women move to reside close to their husbands' families, limits male postmarital migrations and increases those of females. The postmarital migration flow is reversed in matrilocal populations. We thus expect to see higher

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within-population and lower among-population mitochondrial diversity in patrilocal than in matrilocal populations, and the opposite patterns for Y-chromosome.

However, at the local scale, no consensus has been reached on the impact of postmarital residence on uniparental genetic diversity with conflicting results being reported. For instance, mtDNA and Y chromosome genetic patterns assessed respectively from HV1 sequences and 9 short tandem repeats (STRs) are correlated with residence rules in Sino-Tibetan matrilocal and patrilocal populations from northern Thailand (Hamilton et al., 2005; Oota et al., 2001). Similarly in populations from West Timor, uniparental genetic patterns assessed from HV1 sequence and SNPs for mtDNA and 14 STRs and 88 SNPs for Y chromosome are correlated to the matrilocal residence rule (Tumonggor et al., 2014). However, Hmong-Mien patrilocal populations from northern Thailand exhibit comparable levels of mitochondrial (HV1 sequence) and Y chromosome (15 STRs) diversities as Sino-Tibetan matrilocal populations (Besaggio et al., 2007). Similarly, mitochondrial (HV1 sequence) and Y chromosome (6 STRs) diversities are not correlated to postmarital residence rules in Austro-Asiatic and Dravidian populations from India (Kumar et al., 2006). Pygmy populations, which are patrilocal, have mitochondrial (HV1 sequence) and Y chromosome (6 STRs) diversities typical of matrilocal populations (Verdu et al., 2013). Moreover, a study of two populations from Sumatra have found a significantly lower mtDNA diversity (based on complete mtDNA genome sequence) for the matrilocal than the patrilocal population but no difference among them in Y-chromosome diversity (12 SNPs and 12 STRs) (Gunnarsdóttir et al., 2011).

These conflicting results may come from the fact that these studies have focused mainly on the postmarital residence rule without taking into account other ethno-demographic behaviors that may shape populations' genetic diversity (reviewed in Heyer et al., 2012). In particular, the rule of descent (which affiliates individuals to kin groups) may profoundly impact uniparental genetic diversity. Indeed, members of the same patrilineal clan have been shown to be more genetically related for their Y chromosome than random pairs of individuals from the same population (Chaix et al., 2004; Montinaro et al., 2016; Sanchez-Faddeev et al., 2013), showing that descent groups are mirrored into uniparental genetic structures. In addition, descent groups undergo fission and extinction processes, which may reduce the population effective size (Diamond, 1975; Smouse et al., 1981). Such reduction is expected to be sex-specific because of the unilineal nature of descent groups: for instance, patrilineal populations from Central Asia have been shown to have lower male than female effective population sizes (Ségurel et al., 2008). Moreover, these patrilineal populations, who have also a patrilocal residence rule, exhibit lower Y chromosome diversity than nearby populations having a patrilocal residence rule, but a cognatic descent (i.e. no descent groups) (Chaix et al., 2007). This suggests that in harmonious kinship systems (when residence is patrilocal and descent patrilineal, or when residence is matrilocal and descent matrilineal), the residence and the descent rules may act in a synergic way when impacting uniparental genetic diversities. In addition, the practice of polygyny according to which some men marry several women while others do not reproduce generates a higher variance of reproductive success in men as compared to women, thus reducing the male effective population size relatively to the female effective size (Kimura and Crow, 1963). For example, the practice of polygyny had been proposed as an explanation for the reduced Y chromosome diversity in New Guinean populations (Kayser et al., 2003). Moreover, reproductive success can be transmitted from parents to children in a sex specific way, further enhancing the contrast between male and female effective sizes (Heyer et al., 2012). Thus, various sex-specific ethno-demographic factors other than the residence rule could potentially influence uniparental genetic diversity, and it is critical to take them into account in order to understand the impact of social organization on uniparental diversity.

In addition, most of these studies have classified populations according to residence or descent rules based on ethnographic record, which may or may not be strictly followed, without attempting to quantify the actual residence and descent patterns. Such a quantitative and interdisciplinary approach is an essential step towards a better understanding of the influence of social organization on genetic diversity (Destro Bisol et al., 2012; Guillot et al., 2015; Shenk and Mattison, 2011).

Here, we undertake such an interdisciplinary approach by collecting quantitative ethno-demographic data at the individual level as well as uniparental genetic data from 12 Southeast Asian populations exhibiting a wide variety of descent (matrilineal, patrilineal, or cognatic) and residence (matrilocal, patrilocal, or multilocal) rules. All these populations are rural agriculturalists living in tropical areas in Laos and Cambodia. They all cultivate rice in swiddens except for the Khmers who practice wet rice agriculture. They all speak an Austroasiatic language with the exception of the Jarai who speak an Austronesian language. Contrary to most previous studies which focus on a particular component of social organization, this study intends to capture multiple aspects of social organization by analyzing in a quantitative manner post-marital residence as well as descent group structure, and confronting them to uniparental genetic diversity. In particular, we show that both residence and descent patterns are reflected in genetic diversity. A quantitative and global approach of social organization explains genetic diversity more powerfully than discrete categories based on rules and explains apparent discrepancies between residence rules and uniparental genetic diversity. In addition, our study suggests higher social regulation of sex-specific migrations in matrilocal than in patrilocal populations from South-East Asia, which contrasts with observations in Hill Tribes from Thailand (Hamilton et al., 2005).

2 | MATERIALS AND METHODS

2.1 | Sampled populations

Twelve populations from Cambodia and Laos were sampled in 61 villages during 3 field missions carried out between 2011 and 2012: the Tampuan, Jarai, Kacho', Bunong, Khmer, Brao and Kreung from Cambodia and the Khmu', Ramet, Ta-oih, Pacoh, and Prai from Laos (Figure 1). The populations were chosen for their differences in residence and descent rules. Most of them have been the focus of ethnographic

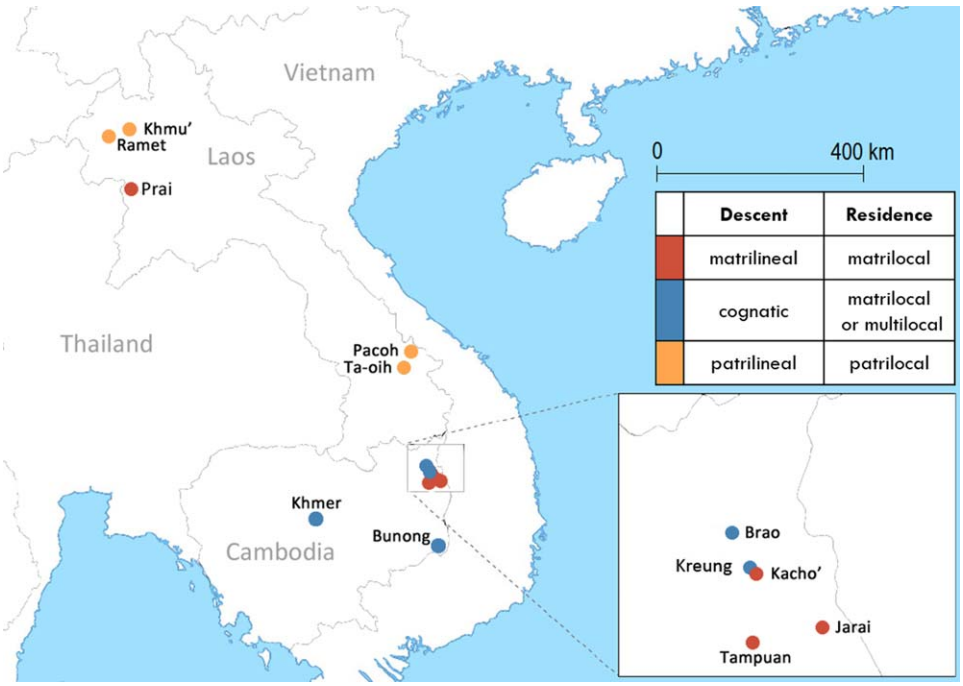

FIGURE 1 Map of sampled populations. The barycenter of the sampled villages for each population is shown. Populations with matrilineal descent and matrilocal residence are represented in red. Populations with cognatic descent and matrilocal or multilocal residence are represented in blue. Populations with patrilineal descent and patrilocal residence are represented in yellow

works, providing description of their social organization (Table 1). The Tampuan, Jarai, Kacho', and Prai have matrilineal descent and matrilocal residence (Bourdier, 2006; Dessaint, 1981; Dournes, 1972; LeBar et al., 1964), the Bunong and the Khmer have cognatic descent and matrilocal residence (Ebihara, 1977; Ledgerwood, 1995; Martel, 1975; UNDP Cambodia, 2010a), the Brao and Kreung have cognatic descent and

TABLE 1 Description of the studied populations with sampling information

Population	Descent rule	Residence rule	Abbreviation (Group)	Sampled villages	mtDNA samples	Y chromosome samples	Ethno-demographic interviews
Tampuan	Matrilineal[a]	Matrilocal[b]	M	8	121	61	65
Jarai	Matrilineal	Matrilocal		6	85	56	56
Prai	Matrilineal	Matrilocal		4	73	38	37
Kacho'	Matrilineal	Matrilocal		3	41	24	27
Bunong	Cognatic[c]	Matrilocal	C	5	49	45	45
Khmer	Cognatic	Matrilocal		5	57	41	44
Brao	Cognatic	Multilocal[d]		6	34	39	39
Kreung	Cognatic	Multilocal		3	34	36	36
Khmu'	Patrilineal[e]	Patrilocal[f]	P	8	43	121	65
Ramet	Patrilineal	Patrilocal		4	21	40	40
Ta-oih	Patrilineal	Patrilocal		4	21	33	34
Pacoh	Patrilineal	Patrilocal		5	40	49	44
Total				61	619	583	532

[a]Matrilineal descent: descent group affiliation is transmitted to the children through the mother.
[b]Matrilocal residence: the husband moved to his wife's natal village after marriage.
[c]Cognatic descent: recognition of descent from both sides of the family in the absence of any specified lines of descent.
[d]Multilocal residence: the couple lives alternatively in the husband's and wife natal villages before settling definitively in one place.
[e]Patrilineal descent: descent group affiliation is transmitted to the children through the father.
[f]Patrilocal residence: the wife moves to her husband's natal village after marriage.

multilocal residence (Baird, 2008; LeBar et al., 1964; Matras-Troubetzkoy, 1983; UNDP Cambodia, 2010b) and the Khmu', Ramet, Ta-oih, and Pacoh have patrilineal descent and patrilocal residence (Evrard, 2006; Izikowitz, 1951; LeBar et al., 1964; Lindell et al., 1979; Schmutz, 2013) (see caption of table 1 for definitions of the terms characterizing social organization).

On the basis of their social organization, the populations were divided into three categories: populations with matrilineal descent and matrilocal residence (M), populations with patrilineal descent and patrilocal residence (P), and populations with cognatic descent rule and either matrilocal or multilocal residence rule (C).

2.2 | DNA samples

Unrelated individuals at the first cousin level with all four grandparents from the same population were sampled. We collected two saliva samples for each individual (4 mL each). Samples were kept in equivalent volume of lysis buffer with 300 μL of 10% SDS and 60 μL of proteinase K (20 mg/mL). DNA was extracted from saliva samples using a standard ethanol precipitation protocol. All participants provided written informed consents and the study was approved by the National Ethic Comities for Health Research in Cambodia and Laos as well as by the Comité Opérationnel pour l'Ethique (CNRS, France).

2.3 | Mitochondrial genome sequencing

We sequenced 619 individuals for the hypervariable region 1 (HV1) of the mtDNA control region from position 16,024 to 16,383 using primer L15925 and HH23 on an ABI 3730XL automated DNA analyzer (Applied Biosystems). Sequences were aligned using GenalysWin v.3.3.40a. The polyC stretch (sites 16,179–16,194) was removed from the aligned sequences before analysis. HV1 sequences are available on GenBank with accession number MG663598 to MG664216.

2.4 | Y-chromosome STR genotyping

We genotyped 588 individuals using the AmpFlSTR Yfiler PCR Amplification Kit (Applied Biosystems) for 17 Y-chromosome short tandem repeat (STR) loci (DYS19, DYS385a, DYS385b, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS438, DYS439, DYS437, DYS448, DYS456, DYS458, DYS635 and Y GATA H4). PCR were performed according to the manufacturer's manual protocol. PCR products were analyzed using an ABI 3130 automated DNA analyzer (Applied Biosystems) and the Genemapper software (Applied Biosystems). Genotypes are provided in table S1, Supporting Information.

Sample sizes per village are listed in Table S2, Supporting Information.

2.5 | Genetic data analysis

Within population haplotype diversity for the mtDNA HV1 sequence and Y chromosome STRs data, as well as mean number of pairwise differences (MNPD) between haplotypes were estimated using Arlequin version 3.5 (Excoffier and Lischer, 2010). We estimated both of these genetic diversity estimators as they are not always concordant and previous studies had found varying results on those estimators (Besaggio et al., 2007; Marchi et al., 2017; Gunnarsdóttir et al., 2011; Tumonggor et al., 2014; Verdu et al., 2013). Mann–Whitney–Wilcoxon tests (MWW) were used to assess differences in haplotype diversity and MNPD between social organizations.

The level of genetic structuration among villages (within each population) was evaluated by computing, among-villages Φst (Excoffier et al., 1992) based on pairwise differences for mtDNA and Y chromosome. It was also evaluated by among-villages Rst based on the number of repeat differences between Y haplotypes (Michalakis and Excoffier, 1996). The three estimators were computed by an Analysis of MOlecular Variance (AMOVA) using Arlequin 3.5 (assigning individuals to their village of residence). Villages with less than 5 sampled individuals were removed from the analysis. The significance of Φst and Rst was assessed using a permutation approach (1,000 permutations of individuals among villages for each population): the *p*-value was defined as the proportion of permutations yielding a higher Φst/Rst value than the one observed.

2.6 | Ethno-demographic data collection

We interviewed 532 individuals, conjointly with their spouse when possible, and collected ethno-demographic information (descent group affiliation, mother tongue, birth village, and residence village) for them, their spouse and their family members (parents, grandparents, siblings, children, and their respective spouses). This procedure allowed us to gather first hand ethno-demographic information for 532 couples (core dataset) and second hand ethno-demographic information for 3,530 couples (extended dataset). We interviewed individuals having all four grandparents from the same population, and similarly so for their spouse, consequently all 532 core couples were endogamous at the population level. The DNA samples were taken from the interviewee, his/her spouse and/or one of his/her children. Sample sizes per village are listed in table S2, Supporting Information.

2.7 | Post–marital residence estimators

We classified the couples into four categories of postmarital residence (Carrasco, 1963; Casselberry and Valavanes, 1976): (i) natolocal when both spouses were born in the same village and resided in it after marriage; (ii) patrilocal if the spouses were born in different villages and the wife moved to her husband's village after marriage; (iii) matrilocal if the spouses were born in different villages and the husband moved to his wife's village after marriage; (iv) neolocal if the couple settled in a different village from their respective natal villages. In this last case, spouses can be born in the same village or in different villages.

We estimated male and female migration rates. The male migration rate corresponds to the sum of the proportions of matrilocal and neolocal couples, and the female migration rate to the sum of the proportions of patrilocal and neolocal couples.

We used logistic regression to assess the influence of social organization (M, P, and C) on proportions of natolocal, neolocal, matrilocal, and patrilocal couples, as well as male and female migration rates. In all

these models, we incorporated individuals' population, village of residence and family as random effects in order to adjust results for potential sample bias linked to the fact that couples of the same population, village or family might share similar postmarital residence behavior. Similar results were found when these random effects were not integrated in the model (results not shown). All generalized linear mixed models were performed with the 'lme4' v1.1–9 package in R (Bates et al., 2015) and *p*-values were obtained using the package 'lmerTest' v2.0–32.

2.8 | Descent group structure estimators

All unilineal populations are organized into clans. Members of the same clan recognize themselves as having a common paternal or maternal ancestor, in patrilineal and matrilineal populations, respectively. Clan affiliation is inherited through the father in patrilineal populations and through the mother in matrilineal populations.

For each unilineal population, we counted the number of clans from the ethno-demographic extended dataset. It was compared between social organizations by MWW test.

We also estimated the proportion of interviewed individuals who knew the clan names of their ascendants (i.e., parents and grandparents). This proportion is here referred as the clan affiliation knowledge rate. This rate may reflect the importance given to the descent affiliation in these populations, and thus could be used as a proxy for the rigidity of clan structure. Clan affiliation knowledge rates were calculated separately for paternal branches (their fathers and paternal grandfathers) and maternal branches (their mothers and maternal grandmothers). We expect better clan knowledge on maternal branches for matrilineal populations and better clan knowledge on paternal branches for patrilineal populations. The influence of social organization on clan affiliation knowledge rates were assessed by logistic regression incorporating the same random effects as models for residence estimators.

All statistical analysis were performed in R v3.2.2 (R Development Core Team, 2008).

3 | RESULTS

To assess the influence of social organization on uniparental genetic diversity patterns, we compared genetic and ethno-demographic estimators collected in three groups of South–East Asian populations: populations with matrilineal descent and matrilocal residence (M), populations with patrilineal descent and patrilocal residence (P), and populations with cognatic descent rule and either matrilocal or multilocal residence rule (C).

3.1 | Genetic diversity estimators

Within population mean number of pairwise differences (MNPD) for the HV1 region of the mitochondrial DNA ranged from 4.6 to 7.2 (fig. S1A, Supporting Information) and was not significantly different between social organizations (p-values > 0.05). However, within population mitochondrial haplotype diversity ranged from 0.81 to 0.99 (Figure 2a), with the Prai exhibiting the lowest mitochondrial diversity, and M populations had a significantly lower mitochondrial haplotype diversity than P populations (p-value $= 0.029$). C populations had intermediate haplotype diversity with no significant differences when compared to either M or P populations (p-value > 0.05).

In terms of among villages genetic differentiation, we observed significant mitochondrial Φst in M but not in P populations with the exception of the Khmu' (Figure 2c). C populations with matrilocal (but not multilocal) residence also exhibited significant among-villages Φst. Thus, we found that all matrilocal populations (with either matrilineal or cognatic descent) had significant levels of mtDNA differentiation among villages.

On the other hand, within population Y chromosome diversity estimators did not show any difference among social organizations: the MNPD ranged from 6.1 to 9.9 and was not significantly different between social organizations (fig. S1B, Supporting Information; p-values > 0.05). The Y haplotype diversity ranged from 0.81 to 1.0, with little variation between populations except for the Pacoh who had by far the lowest diversity (Figure 2b). We observed no significant difference between social organizations (p-value > 0.05).

In addition, very low Y chromosome Rst were observed among villages in all populations (Figure 2d), suggesting a lack of Y chromosome structuration at the village level. The Khmu' were the only population to exhibit significant Rst (p-value $= 0.013$). Similarly, among villages Y chromosome Φst were low in most of the populations (Fig. S2, Supporting Information), except for the Kacho', Khmer, Khmu', and Ramet.

We checked that the lack of signature of social organization on Y chromosome diversity estimators did not result from a saturation issue in relation with the high number of STRs (17 STRs) used in this study, which might yield to a myriad of haplotypes nearly all different from each other, thus masking the potential impact of social organization. Thus, we replicated our analyses with a reduced set of STRs [the 9 STRs of the minimal haplotype (Kayser et al., 1997)] and confirmed that similar results were found (results not shown).

3.2 | Influence of residence patterns on genetic diversity

We estimated the proportions of natolocal, matrilocal, patrilocal, and neolocal couples in each population for the extended dataset (fig. S3A, Supporting Information) and the core dataset (fig. S3B, Supporting Information). In each population, the core dataset exhibited a lower proportion of natolocal couples than the extended dataset (on average 0.52 vs. 0.74). This lower proportion could be explained by a recent transition towards lower natolocality in the current generation (the extended dataset comprises a larger proportion of elder people than the core data set) or by a memory bias (erroneous assignations of birth places for parents and grandparents by the interviewee). However, the relative proportion of neolocal, patrilocal, and matrilocal couples were similar in the core and extended datasets for 10 out of 12 populations (χ^2 test p-value > 0.05), and conclusions drawn from both datasets were similar. Hence, we focused here on the results provided by the extended dataset.

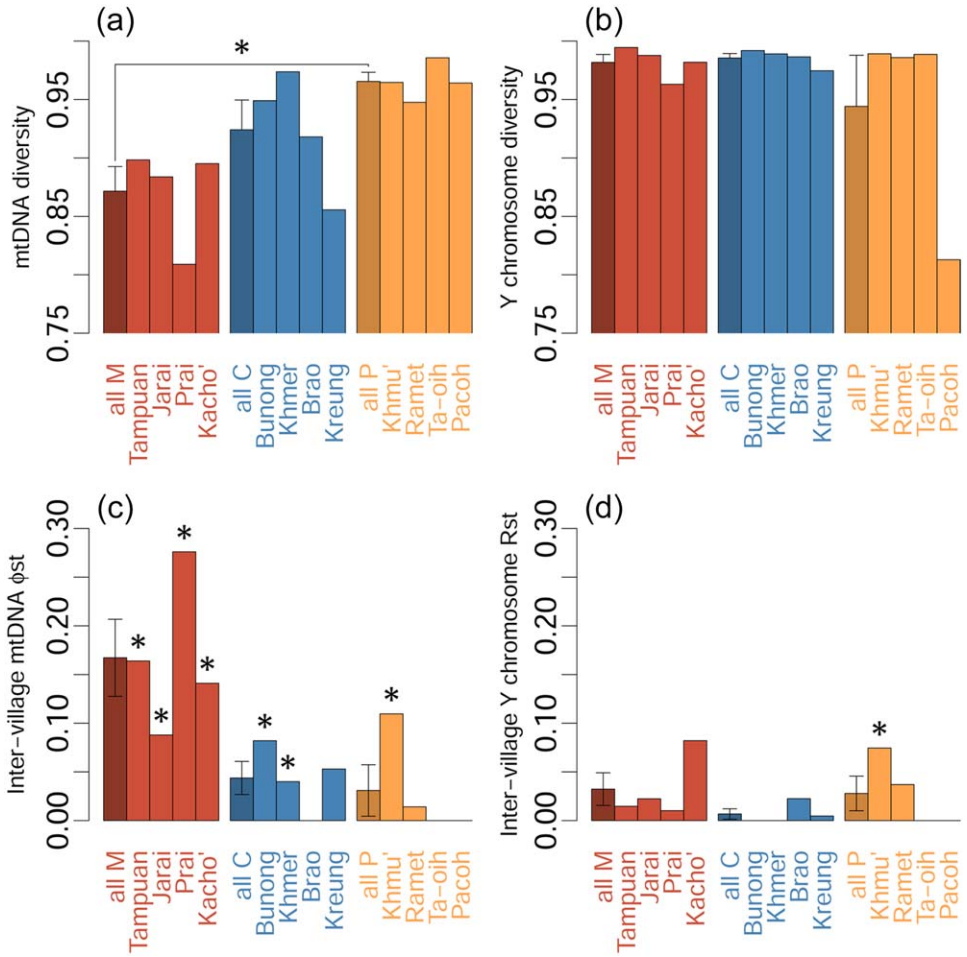

FIGURE 2 Uniparental genetic estimators. (a) mtDNA haplotype diversity; (b) Y chromosome haplotype diversity; (c) Inter-village mtDNA Φst based on pairwise differences between haplotypes; (d) Inter-village Y chromosome Rst based on repeat number differences. The first (darker) bar in each group represents the mean in each group with standard error. M populations are represented in red, C populations in blue and P populations in yellow. Asterisks indicate statistical significance (p-value < 0.05) assessed by MWW tests (a, b) or permutation tests (c, d)

Natolocality was the major type of residence in every population, ranging from 0.47 to 0.92, although it was lower in P populations than in M (p-value $=0.011$) and C populations (p-value $= 0.037$, fig. S3A, Supporting Information).

As expected, M and C populations had a higher proportion of matrilocal couples than P populations (fig. S3A, p-value $< 10^{-3}$ and p-value $= 0.014$, respectively). On the other hand, P populations had a higher proportion of patrilocal couples than M (p-value $< 10^{-3}$) and C populations (p-value $< 10^{-3}$), thus confirming the residence rules described in ethnographical studies (fig. S3A, Supporting Information). Proportion of neolocal couples was lower in M populations than in C (p-value $< 10^{-3}$) and P populations (p-value $< 10^{-3}$).

We estimated male and female inter-villages migration (Figure 3a, b). As expected, female migration rates were significantly different among social organizations, with P populations having the highest rate compared to M and C populations. C populations had also a higher female migration rate than M populations (all three comparisons p-value $< 10^{-3}$). On the other hand, no differences in male migration rates were observed across social organizations (p-value > 0.05 for all 3 comparisons).

Finally, female migration rate between villages correlated positively with mitochondrial haplotype diversity (Figure 3c, Spearman's $\rho = 0.71$, p-value $= 0.012$) and negatively with among villages Φst (Figure 3e, Spearman's $\rho = -0.76$, p-value < 0.01). No correlation was found between mitochondrial MNPD and female migration rate (fig. S1C, Supporting Information Spearman's $\rho = 0.40$, p-value $= 0.20$). On the other hand, we did not observe significant correlations between male migration rate and Y chromosome haplotype diversity (Figure 3d Spearman's $\rho = 0.098$, p-value $= 0.77$), MNPD (Figure S1D, Supporting Information Spearman's $\rho = -0.05$, p-value $= 0.89$), or among villages Rst (Figure 3f, Spearman's $\rho = 0.13$, p-value $= 0.68$) and these results were robust to the removal of the Pacoh who had a much lower Y chromosome haplotype diversity than other populations.

3.3 | Influence of descent group structure on genetic diversity

We compared the number of clans of each population. For M populations, Prai had a much higher number of clans (47) than the other populations (9, 8, 17 in the Tampuan, Jarai, and Kacho', respectively). Pacoh

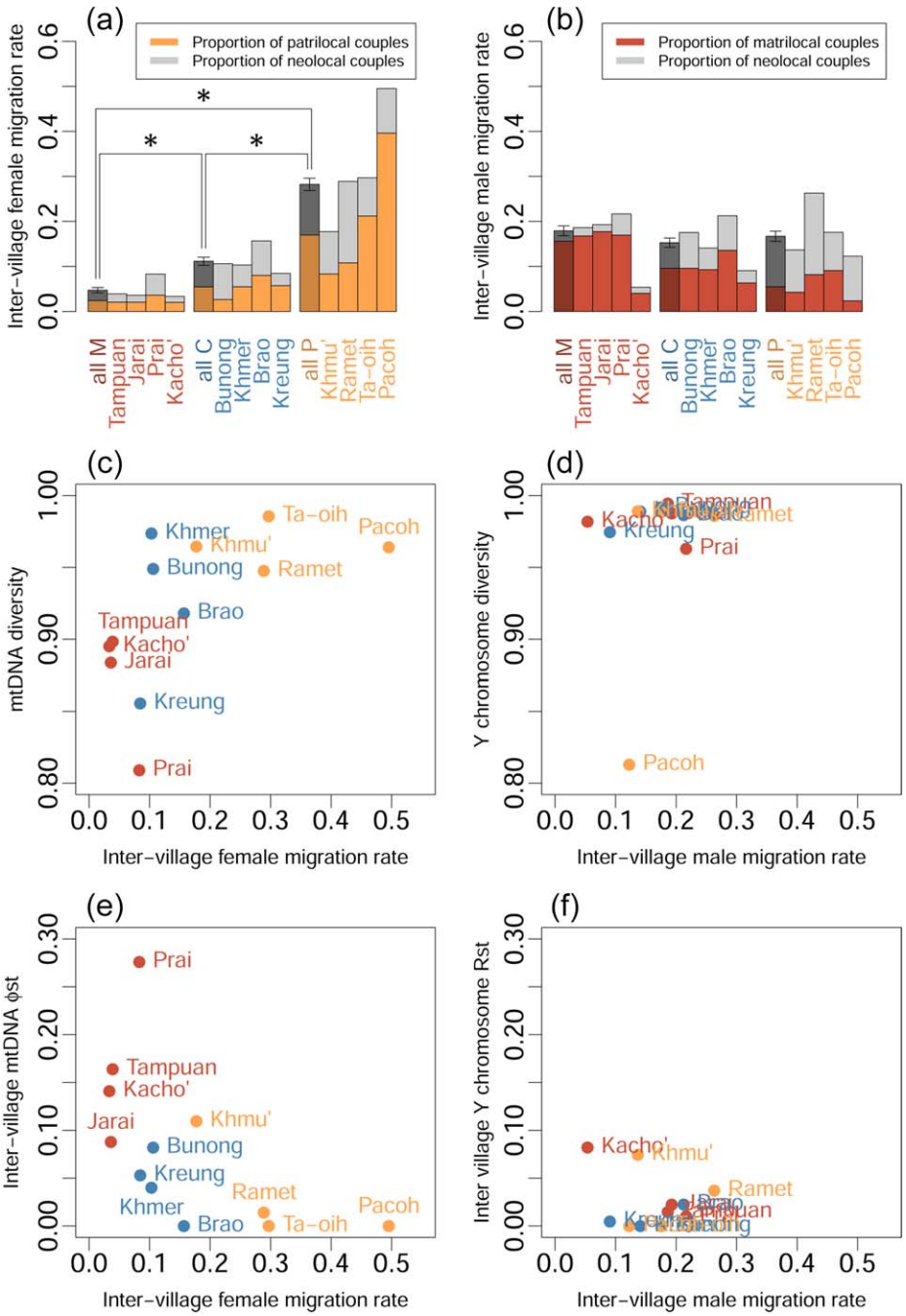

FIGURE 3 Sex-specific inter-village migration rates estimated from our ethno-demographic data on 3,530 couples (extended data set) and correlation with genetic estimators: (a) Female migration rate; (b) male migration rate. The first (darker) bar in each group represents the mean in each group with standard error. Asterisks indicate statistical significance (p-value < 0.05) assessed by logistic regression model; (c) female migration rate against mtDNA diversity (Spearman's $\rho = 0.71$, p-value $= 0.012$); (d) male migration rate against Y chromosome diversity (Spearman's $\rho = 0.098$, p-value $= 0.77$); (e) female migration rate against mtDNA Φst (Spearman's $\rho = -0.76$, p-value < 0.01); (f) male migration rate against Y chromosome Rst (Spearman's $\rho = 0.13$, p-value $= 0.68$). M populations are represented in red, C populations in blue, and P populations in yellow

also had a higher number of clans (57) as compared to the other P populations (17, 11, and 29 in Khmu', Ramet, and Ta-oih, respectively). There was no significant difference in the number of clans between M and P populations (p-value $= 0.38$) (Figure 4).

We further explored differences in descent group structure between populations by comparing the clan affiliation knowledge rate of each population on maternal and paternal branches. As expected, all matrilineal populations had a higher clan affiliation knowledge on the maternal branches than on the paternal branches (Figure 4a). The opposite was true for patrilineal populations except for the Khmu' who knew both branches similarly well. Moreover, M populations had a significantly higher rate of clan affiliation knowledge on their maternal

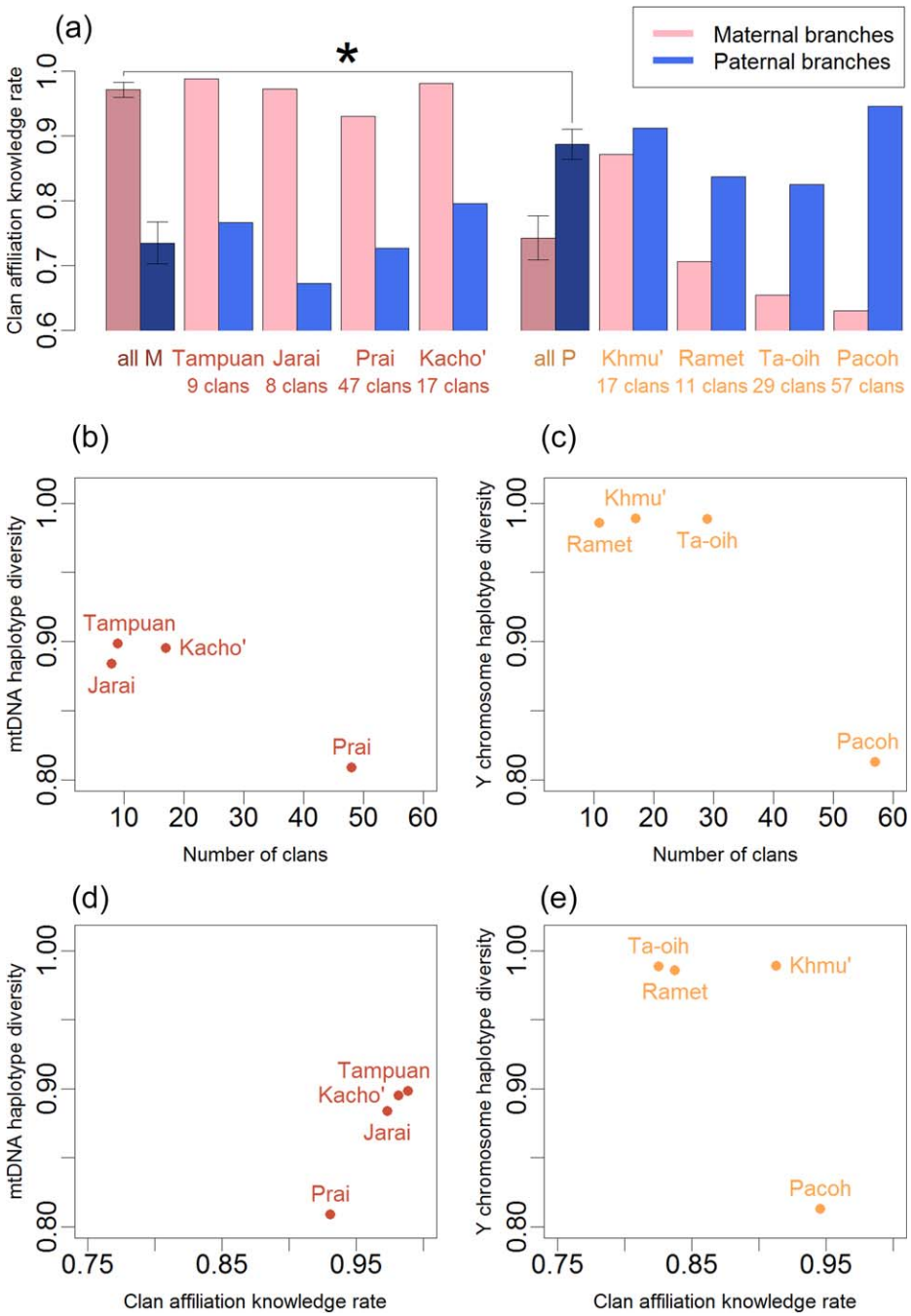

FIGURE 4 Descent group structure estimators and their relationship with genetic diversity. (a) Clan affiliation knowledge rate. Pink bars represent knowledge rate on maternal branches (mothers and maternal grandmothers of the interviewee and of his/her spouse), blue bars represent knowledge rate on paternal branches (fathers and paternal grandfathers of the interviewee and of his/her spouse). The first (darker) bars of each group represent the mean knowledge rate with standard error in each group. Asterisks indicate statistically significant differences between social organizations obtained from the logistic regression model (p-value <0.05); (b) mtDNA haplotype diversity against number of clans in M populations; (c) Y chromosome haplotype diversity against number of clans in P populations; (d) mtDNA haplotype diversity against clan affiliation knowledge rate on the maternal branches in M populations; (e) Y chromosome haplotype diversity against clan affiliation knowledge rate on the paternal branches in P populations

branches than P populations had on their paternal branches (0.97 vs. 0.89; p-value < 0.01), suggesting a higher rigidity of the clanic structure in M than in P populations.

For both M and P populations, we observed that a higher number of clans, as observed in the Prai and the Pacoh, was associated with lower mitochondrial and Y chromosome haplotype diversity, respectively (Figure 4b,c). On the other hand, no consistent pattern was observed between the clan knowledge of ascendants and haplotype diversity across M and P populations (Figure 4d,4e).

4 | DISCUSSION

Our investigation of uniparental genetic patterns in South-East Asian populations with various social organizations showed that the mitochondrial genetic patterns were consistent with the expected effects of matrilocality and matrilinearity (M), whereas Y chromosome genetic patterns were not consistent with the expected effects of patrilocality and patrilineality (P). Indeed, while mtDNA haplotype diversity was lower and inter-village genetic distances higher in M than in P populations, neither reduction in Y chromosome haplotype diversity nor increase in inter-village genetic distances were observed in P populations compared to M populations. These findings are similar to uniparental genetic patterns observed in matrilocal and patrilocal populations from Sumatra (Gunnarsdóttir et al., 2011). Cognatic (C) populations exhibited genetic estimators intermediate between M and P populations.

Interestingly, mitochondrial mean number of pairwise differences was not significantly different between social organizations contrary to mitochondrial haplotype diversity. This observation is consistent with several previous studies investigating the impact of social organization on genetic diversity and that did not find correlation between haplotype diversity and mean number of pairwise differences (Marchi et al., 2017; Gunnarsdóttir et al., 2011). Thus, it suggests that social organization impacts haplotype diversity but seems to leave no signature, or inconsistent signatures, on mean number of pairwise differences.

It is usually assumed that matrilocal populations have higher male migration rates and lower female migration rates compared to patrilocal populations (Besaggio et al., 2007; Gunnarsdóttir et al., 2011; Kumar et al., 2006; Oota et al., 2001) and we usually expect to observe sex-specific genetic signature in accordance with this. For Thailand Hill Tribes, this assumption seems to be accurate (Hamilton et al., 2005; Oota et al., 2001). However, our ethno-demographic data showed that this is not the case for the populations we sampled in South-East Asia. While female migration rate did vary with social organization and was correlated to mitochondrial patterns, male migration rate did not vary with social organization: the same proportion of men migrated away from their birth village in P populations and in M populations. We propose that this lack of difference in male migration rates between social organizations is the main reason for the lack of difference in Y chromosome diversity estimators.

Before going further, we should underscore that populations described as patrilocal by previous ethnographic works had indeed an excess of patrilocal couples (in comparison to matrilocal and neolocal couples), confirming their classification into P populations. However, our ethno-demographic dataset highlighted a higher residence flexibility in P populations than in M populations. Indeed, P populations tolerated a higher proportion of matrilocal couples than the proportion of patrilocal couples tolerated by M populations: in P populations the proportion of matrilocal couples divided by the proportion of patrilocal and matrilocal couples was 23.1% versus 14% for the proportion of patrilocal couples divided by the same denominator in M populations. Consequently, male migrations were increased in P populations in comparison to what would be expected under a stricter patrilocal rule.

In addition, a higher proportion of neolocal couples was observed in P populations (0.11) in comparison to M populations (0.024, p-value $< 10^{-3}$). Consequently, P populations had more frequent inter-villages migration, for both males and females, as compared to M populations. This higher proportion of neolocal couples in P than in M populations was observed (p-value < 0.01) even when estimated only on the oldest generations of our dataset (i.e., parents and grandparents). This argues for the fact that this behavior existed before recent political and social changes. Previous ethnographic works on Khmu' and Ramet showed that a house or a group of houses may move to a new village, and their members may initiate or integrate a new lineage, through a ritual (Evrard, 2006), suggesting that such flexibility may be a common practice in these patrilineal populations.

Thus, such increased flexibility (tolerance for matrilocality and neolocality) in P populations enhanced male migrations in P populations, making them as frequent as in M populations, despite the patrilocal residence rule. Consequently, this analysis showed that patrilocality and matrilocality are not just the opposite sides of the same coin, but different regulatory processes modulate male and female migration rates in these populations.

Interestingly, our higher residence flexibility for P than for M populations contrasted with the tighter social regulation observed in patrilocal compared to matrilocal Hill Tribe populations from Thailand (Hamilton et al., 2005). More precisely, in this study, the authors estimated male and female migration rates from mitochondrial (HV1 sequence) and Y chromosome (9 STRs) genetic data using an approximate Bayesian computation (ABC) method. They showed that females moved ~15 times more than males in patrilocal populations while males only moved 1.3 times as much as females in matrilocal populations. Consequently, the patrilocal Hill Tribe populations seem to follow their residence rule more strictly than the matrilocal Hill Tribe populations. These contrasted observations between Hill Tribe populations and the matrilocal and patrilocal populations studied in this paper could correspond to genuine differences existing between these unilineal populations depending on the socio-cultural and political context. Alternatively, they could result from different study scales [we estimated migration rates between villages within population while Hamilton et al. (2005) focused on migration rates between populations] or to different time scales (our migration rates reflect contemporary rates, while migration rates estimated from genetic data are more likely to reflect long-term rates).

Moreover, our data highlighted that the descent rule, a social rule largely ignored in population genetic studies, could also influence the genetic diversity. Indeed, the Prai had a singularly low mtDNA haplotype diversity while having no reduction of female migration rate in comparison to other M populations. Likewise, the Pacoh had a low Y chromosome haplotype diversity while having no reduction in male migration rate in comparison to other P populations. These reductions in uniparental genetic diversity could be associated with the larger number of clans observed in these two populations in comparison to other P and M populations. It had already been shown that the descent group structure can influence genetic diversity patterns (Chaix et al., 2007; Montinaro et al., 2016; Sanchez-Faddeev et al., 2013; Ségurel

et al., 2008). In Central Asia, Y chromosome diversity is reduced in patrilineal populations in comparison to cognatic populations (both having patrilocal residence) (Chaix et al., 2007). The dynamics of lineal clan fissions in which a clan splits into two clans regrouping closely related individuals, combined with extinctions of patrilineal clans, is likely to be responsible for this reduction in Y chromosome diversity. Theoretical works from Smouse et al. (1981) have indeed showed that lineal fissions combined with clan extinctions may decrease the effective size of the population by a factor up to 4. In the South-East Asian populations studied here, clans in M and P populations such as Jarai and Khmu' have been documented as staying stable over time and thus seems to not undergo lineal fissions (Dournes, 1972; Evrard, 2006). However, in Pacoh and Prai for which clan dynamics have not been documented, the much higher number of clans suggests a lineal fission process, which may be responsible for the lower uniparental haplotype diversity observed in these two populations. However, it should be noted that other sex specific factors such as sex differences in variance of reproductive success or heritability in reproductive success could also play a part in shaping the uniparental genetic patterns by influencing the level of genetic drift on uniparental DNA (Heyer et al., 2012). Further work on the reproductive history of the individuals is needed in order to assess the variance in reproductive success among individuals and its heritability across generations. However, polygyny, one of the main factor linked to sex-specific variance in reproductive success was found at low rates in all 12 populations. From our ethno-demographic dataset, we estimated that 1.4% (SD = 3.0%) of men are in a polygynous relationship in average in each population and thus it is doubtful that polygyny had a meaningful impact in the studied populations.

Finally, some studies suggested that the choice of the HV1 sequence of the mitochondrial DNA and of Y chromosome STRs may not be optimal to characterize the genetic signature of social organization, and proposed that it was better to rely on the complete mitochondrial genome and on sequences from nonrecombining Y-chromosome fragments (Gunnarsdóttir et al., 2011; Lippold et al., 2014), as well as on X/autosome diversity ratios (Ségurel et al., 2008). However, focusing on the HV1 sequence of the mitochondrial DNA, we were able to detect differences between populations that correlate to their social organizations, and notably to the female migration rate. In addition, the lack of difference in Y chromosome diversity among populations having different social organizations is consistent with the absence of difference in male migration rates among them. Thus, we are confident that the markers we used were powerful enough and represent a suitable option for our study scope.

To conclude, our study shows that fine quantification of social organization was necessary to better grasp its impact on genetic diversity and solve apparent discrepancies between social rules and genetic patterns as some authors have previously suggested (Destro Bisol et al., 2012; Guillot et al., 2015; Marks et al., 2012; Shenk and Mattison, 2011; Wilkins, 2006). Moreover, it highlights the need to consider the different components of social organization altogether (residence but also descent and alliance rules), in order to better understand its impact on genetic diversity.

5 | ETHICS

All participants provided written informed consents and the study was approved by the National Ethic Comities for Health Research in Cambodia and Laos as well as by the Comité Opérationnel pour l'Ethique (CNRS).

6 | DATA DEPOSITION

Mitochondrial DNA HV1 sequences are available on GenBank with accession number MG663598 to MG664216. Y chromosome STR genotypes are provided in table S1, Supporting Information.

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AUTHORS' CONTRIBUTIONS

R.C., S.P. and B.T. initiated the project; R.C., S.P., R.L, S.L., O.E., F.B. G. D and C.M. contributed to the ethno-demographic and genetic sampling; S.L. and C.M. carried out the lab work; G.L., B.A. and R.L. analyzed the data; G.L., R.C. and S.P. wrote the paper. All authors gave final approval for publication.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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