

HIV-1 epidemic in Warao Amerindians from Venezuela: spatial phylodynamics and epidemiological patterns

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Objectives: We previously reported HIV-1 infection in Warao Amerindians from Venezuela. The aim of this study was to evaluate the extent and the dynamic of HIV-1 dissemination in eight Warao communities.

Design and Setting: HIV-1 infection was evaluated in 576 Warao Amerindians from the Orinoco Delta. Partial HIV-1 *pol* sequences were analyzed to reconstruct the spatiotemporal and demographic dynamics of the epidemic.

Results: HIV-1 antibodies were present in 9.55% of Warao Amerindians, ranging from 0 to 22%. A significantly higher prevalence was found in men (15.6%) compared with women (2.6%), reaching up to 35% in men from one community. All but one isolates were classified as subtype B. Warao's HIV-1 subtype-B epidemic resulted from a single viral introduction at around the early 2000s. After an initial phase of slow growth, the subtype B started to spread at a fast rate (0.8/year) following two major routes of migration within the communities.

Conclusion: A dramatic high prevalence was documented in almost all the communities of Warao Amerindians from the Orinoco Delta tested for HIV-1 infection. This epidemic resulted from the dissemination of a single HIV-1 subtype B founder strain introduced about 10 years ago and its size is probably doubling every year, creating a situation that can be devastating for this vulnerable Amerindian group.

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Introduction

In 2009, UNAIDS estimated an adult prevalence of HIV-1 of 0.5% in Central and South America. The Venezuelan government estimates the prevalence in the general population at less than 1% [1,2]. There are few available reports of HIV in Amerindian populations of Latin America

[3–7]. In 2007, the Venezuelan Red Cross identified some cases of HIV in the community of San Francisco de Guayo (Villalba J, personal communication). Recently, other cases were identified in individuals from four communities [8]; that study showed that at least two independent introductions of HIV-1 occurred in this population, one of subtype B and another one of subtype C.

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Warao Amerindians live in the Orinoco Delta, a remote-region furrowed by hundreds of streams and rivers [9]. Grouped in isolated villages, Waraos have almost no access to medical care and represent a highly vulnerable population with huge health, nutritional and social problems [10,11]. As of the 2001 Venezuelan National Census, there were 26 080 Waraos residing in Venezuela [12], representing the second largest indigenous tribe in Venezuela, a country that comprises 2% of indigenous population [13]. Traditionally, most of the Warao were swamp and jungle foragers [9]. Today, most of them live in extreme poverty conditions, developing fishing activities, subsistence agriculture or working for government missions. Many of them have seminomadic habits, living for short periods in slums around 'Creole' villages where they are exposed to many potentially troublesome activities such as a garbage dump sorting activity or prostitution [14,15]. The aim of this study was to evaluate in detail the extent and the dynamic of HIV-1 dissemination in different Warao Amerindians communities.

Methods

Ethics approval

Written informed consent that was verbally translated into the Warao language was obtained from the

participants. Consent of the villages was obtained through meetings with Warao community councils. Project was approved by Servicio de Atención y Orientación al Indígena (SAOI) (Office in charge of Indigenous Health in Delta Amacuro State), Regional HIV Programme, the local Office of Health Programs of Delta Amacuro State and the Ethical Committee of Instituto Venezolano de Investigaciones Científicas in Caracas, Venezuela. The present study is in compliance with the Organic Act of People and Indigenous Communities of Venezuela. HIV-positive patients identified were reported to the Regional and National HIV Programmes. A furlough to publish this study was given by the local Office of Health Programs of the Delta Amacuro State and SAOI. Venezuelan Ministry of Health and Pan American Health Organization received reports of this study previous to publication.

Study population

An epidemiological cross-sectional study was carried out in eight Warao villages in the Lower Orinoco Delta (LOD): San Francisco de Guayo, Jobure de Guayo, Ibuiruiña, Jeukubaka, Jobotoboto, Usidu and Isla de Jobure (Fig. 1). All individuals over 10 years willing to participate were invited to participate in the study. Children from positive patients were sampled under parental consent (not included in prevalence analysis). Samples from known HIV-positive patients from other

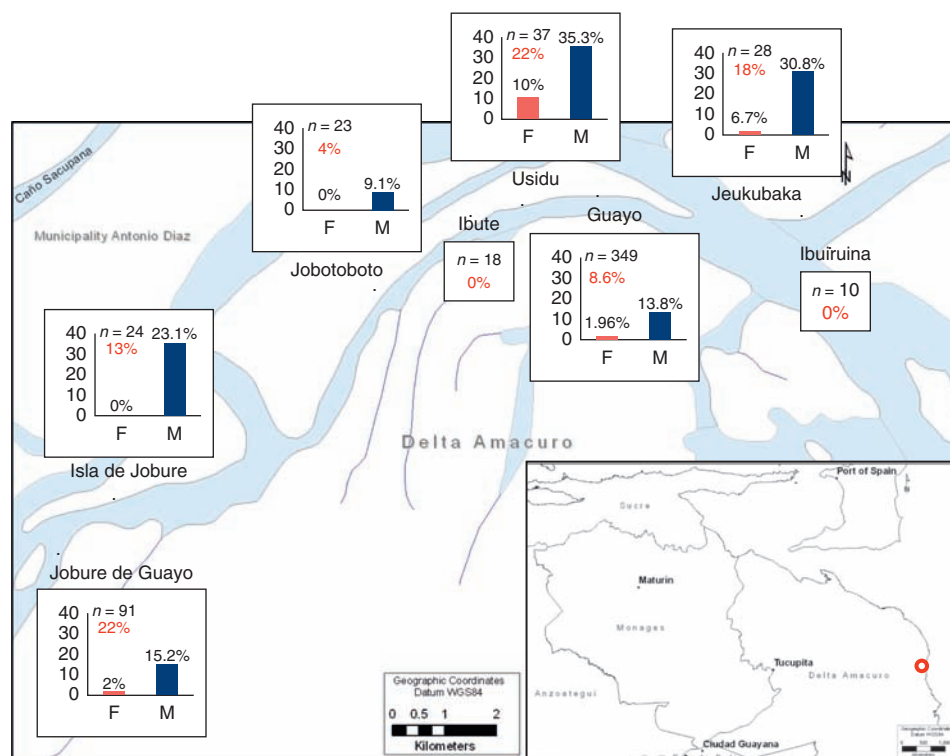


Fig. 1. HIV-1 prevalence in Warao communities from the Orinoco Delta Prevalence study was carried out in communities shown inside the box. Map shows point prevalence of HIV-1 in the studied communities (numbers in black and general prevalence in red inside the boxes). Bar graphs show the prevalence in men (blue bar) and women (red bar) populations.

four communities (Nabasanuka, Caño Yeri, Kuberuna and Cambalache) were also collected. HIV-positive patients underwent physical examinations, disease stratification, and an epidemiological interview (simultaneously translated to Warao language by Spanish–Warao bilingual native interpreters) about transmission category, migratory status, and disease knowledge.

Determination of HIV-1 infection and molecular characterization

Blood samples were taken and separated in the field. All samples underwent Abbott DetermineHIV-1/2 rapid-assay to detect HIV-infection. Positive patients were confirmed by ELISA and western blot. HIV-1 RNA was detected by RT-nested PCR for plasma or direct nested PCR from proviral DNA and amplicons of the partial *pol* genomic region were sequenced as previously described (nucleotides 2057–3587 relative to HXB2 genome) [8]. Nucleotide sequence data have been deposited into the GenBank database under the accession numbers KC133213–KC133265.

Phylogenetic analysis

Maximum likelihood tree was reconstructed with program PhyML [16] using an online web server [17] under the GTR+I+ Γ 4 nucleotide substitution model, selected using the jModeltest program [18]. Heuristic tree search was performed using the Subtree pruning and regrafting branch-swapping algorithm and the reliability of the obtained topology was estimated with the approximate likelihood ratio test (aLRT) [19] based on a Shimodaira–Hasegawa-like procedure. Trees were visualized using the FigTree v1.3.1 program.

Phylogeographic and population dynamics analyses

The spatiotemporal and demographic dynamics of dissemination of HIV-1 subtype B in Waraos Amerindians was reconstructed using the Bayesian Markov Chain Monte Carlo (MCMC) approach as implemented in BEAST v1.6.2 [20,21]. Analyses were initially performed using the GTR+I+ Γ 4 nucleotide substitution model, an uncorrelated Lognormal relaxed molecular clock model [22], and an informative substitution rate prior for the *pol* genomic region (1.5×10^{-3} – 2.5×10^{-3} substitution/site per year). Migration events throughout the phylogenetic history were identified by applying a standard discrete Bayesian phylogeographic model [23]. Migratory events were summarized using the cross-platform Spatial Phylogenetic Reconstruction of Evolutionary Dynamics application [24] and viewed using the cartographic tools of the Venezuelan Ministry of Environment and generated by Arcgis version 9.3. Change in effective population size through time and estimates of the population growth rate were obtained using the Bayesian Skyline [25] and the expansion growth coalescent tree priors. MCMC chains were run for 50×10^5 generations and adequate chain

mixing was checked, after excluding an initial 10%, by calculating the effective sample size using TRACER v1.4 program. Maximum clade credibility (MCC) trees were summarized from the posterior distribution of trees with TreeAnnotator and visualized with FigTree v1.3.1.

Statistical analysis

To assess the relationship between categorical variables and HIV-1 prevalence, odds ratios and 95% confidence intervals (CI) were calculated by univariate logistic regression analysis. The significance of differences between proportions was assessed using Pearson's χ^2 test. A *P* value of less than 0.05 was considered significant. Concordance between classification of individuals according subtribes and phylogenetic clusters was assessed using the Cohen's Kappa (κ) coefficient.

Results

A total of 576 individuals were tested for HIV-1 infection, representing 37.4% of the total adult population of eight Warao communities, according to the last Venezuelan census in 2001 [12]. Men and women comprised 53.3% (307) and 46.7% (269) of the participants, respectively. Age distribution was: 11% (65) above 50 years old, 34% (195) between 31 and 50 years old, 31% (180) between 18 and 30 years old, 23% (135) between 10 and 17 years old, and only one individual was under 10 years old. A total of 55 samples from six communities were positive for HIV by rapid-test (9.55%), being confirmed all but one, who died with AIDS's symptoms before the second sampling, by confirmatory tests. HIV-1 prevalence ranged from 0 to 35.3% among adult men in the different communities (Fig. 1). In univariate analysis, this prevalence was significantly higher in Usidu (21.6%) when compared with other communities (Table S1, <http://links.lww.com/QAD/A326>). The prevalence was also significantly higher among men (15.6%) compared with women (2.6%), and among individuals aged 18–30 years (19%) compared with other age groups combined (Table S1, <http://links.lww.com/QAD/A326>).

Most of the HIV-1-infected patients were asymptomatic (58%), whereas 26% presented with B-symptoms according to CDC 1993 AIDS Staging System (CDCASS). Diarrhea was the most prevalent B symptom found (64% of patients staged as B), followed by fever for more than 1 month (36%) and herpes zoster (21%). Nine patients (16%) were classified as C. The questionnaire performed on HIV-infected individuals showed that same-sex intercourse and bisexuality were frequent among them (Table 1).

The partial HIV-1 *pol* genomic region of 53 out of 55 HIV-positive Warao Amerindians from Guayo, Jobure de Guayo, Usidu, Jobotoboto, Jeukubaka and Isla de Jobure

Table 1. HIV-1-positive patient characteristics.

Characteristic	Frequency (%)
Sex (<i>n</i> = 55)	
Men	48 (87)
Women	7 (13)
Age (Mean $\pm$ SD)	27.9 $\pm$ 11.5
Age distribution (<i>n</i> = 55)	
Adolescents (10–17 years)	7 (13)
Young adults (18–30)	29 (53)
Adults (31–50)	16 (29)
Elders (>50)	3 (5)
Socio-anthropological characteristics (<i>n</i> = 55)	
Illiteracy	28 (51)
School completion	2 (4)
Practice of fishing and subsistence farming	34 (62)
Risk factors (<i>n</i> = 45)	
Same-sex intercourse	30 (67)
Paid sex	5 (11)
Intercourses with sexual workers	7 (16)
One-time casual sexual encounters	16 (36)
Sexual encounters during travels	12 (27)
Sexual orientation (<i>n</i> = 49)	
Heterosexual	23 (46)
Homosexual	6 (12)
Bisexual	20 (41)
Transgender	3 (6)
Age of sexual initiation (mean $\pm$ SD)	14 $\pm$ 4
Sexual partners per year (mean $\pm$ SD)	3.8 $\pm$ 5.5
Disease knowledge (<i>n</i> = 49)	
Some knowledge about HIV/AIDS	19 (39)
Knowledge about HIV transmission	8 (16)
Knowledge about HIV prevention strategies	12 (25)
Use of barrier methods	4 (8)
Travelling history (<i>n</i> = 55)	
Seminomadic behaviors (living up to five communities)	12 (22)
Common travels* to Tucupita (Capital of Delta Amacuro State)	27/49 (55)
Common travels* to other communities	45
Travel to other states inside Venezuela	32/49 (65)
Have been to Cambalache	19/49 (53)

were amplified and combined with five HIV-1 *pol* sequences from Warao living in others four communities (Nabasanuka, Caño Yeri, Kuberuna and Cambalache). All HIV-1 samples were subtyped as B, except one classified as subtype C (data not shown). The maximum likelihood phylogenetic analysis showed that all HIV-1 subtype B sequences from Warao segregates in a highly supported (*aLTR* = 0.95) monophyletic clade nested within the Venezuelan subtype B radiation (Fig. 2a), thus, supporting a single introduction of subtype B in this isolated population. The single Warao HIV-1 subtype C isolate was not phylogenetically related to other subtype C isolates previously identified in South America (data not shown).

Bayesian analysis indicate that the Waraos subtype B clade most probably originated at around 2002 (95% highest posterior density, HPD: 1998–2005) and placed the most

probable root location of that viral lineage in Guayo (posterior state probability, *PSP* = 0.38), Jeukubaka (*PSP* = 0.28) and Usidu (*PSP* = 0.15) (Fig. 2b). However, as those localities are the communities exhibiting the highest numbers of HIV-1 cases, this assumption may be due to a sampling bias. The maximum likelihood and Bayesian MCC trees show that subtype B sequences from Warao branched in two reciprocally monophyletic clades, representing two main transmission routes (Fig. 2b). One route, called Guayo, most probably started in the Guayo community (*PSP* = 0.76) at around 2005. From Guayo the virus was disseminated to Isla de Jobure, Jobure de Guayo, and Usidu, and from Usidu to Jobure de Guayo, Jobotoboto and Kuberuna (Figs 3 and 4). The other route, called Jeukubaka, most probably started in the Jeukubaka community (*PSP* = 0.68) also at around 2005. From there the virus was disseminated to Cambalache, Isla de Jobure, Nabasanuka and Usidu, and from Nabasanuka to Caño Yeri (Fig. 2b and 3). The Cohen's κ correlation between subtribal classification of the communities and clusters was 0.903 (95% CI: 0.771–1.035). Although the HIV-1 epidemic in Usidu seems to be the result of multiple subtype B introductions from Guayo followed by subsequent local expansion of those viruses, the epidemic in Jobure de Guayo mainly resulted from the local dissemination of one founder viral strain introduced from Guayo (Fig. 2b). This analysis further revealed that the connection between both transmission networks seems to be minimal. With the exception of one transmission event from Jeukubaka to Usidu and another one from Guayo to Isla de Jobure, no other viral transmission were observed between communities from the Guayo and Jeukubaka networks (Fig. 2b and 3).

The Bayesian skyline plot analysis for demographic history reconstruction supports a two-phase model for viral dissemination in the Warao communities tested: an initial phase of slow dissemination followed by a more recent phase of exponential growth that started at around 2005, coinciding with the arrival of the virus in Guayo and Jeukubaka and its subsequent dispersion to other communities (Fig. 4a). This demographic pattern coincides with a model of expansion growth that was then used to estimate the growth rate of the HIV-1 epidemic in the Warao communities. According to the expansion model, the HIV-1 subtype B spread in the Waraos at a median rate of 0.81 year⁻¹ (95% HPD: 0.42–1.19 year⁻¹) between 2005 and 2012, which corresponds to a median epidemic doubling time of 0.87 year (95% HPD: 0.58–1.44 year⁻¹) (Fig. 4b).

Discussion

The first HIV-cases in Warao Amerindians were identified in 2007 in individuals presenting with AIDS symptoms. A previous study of our group showed that at

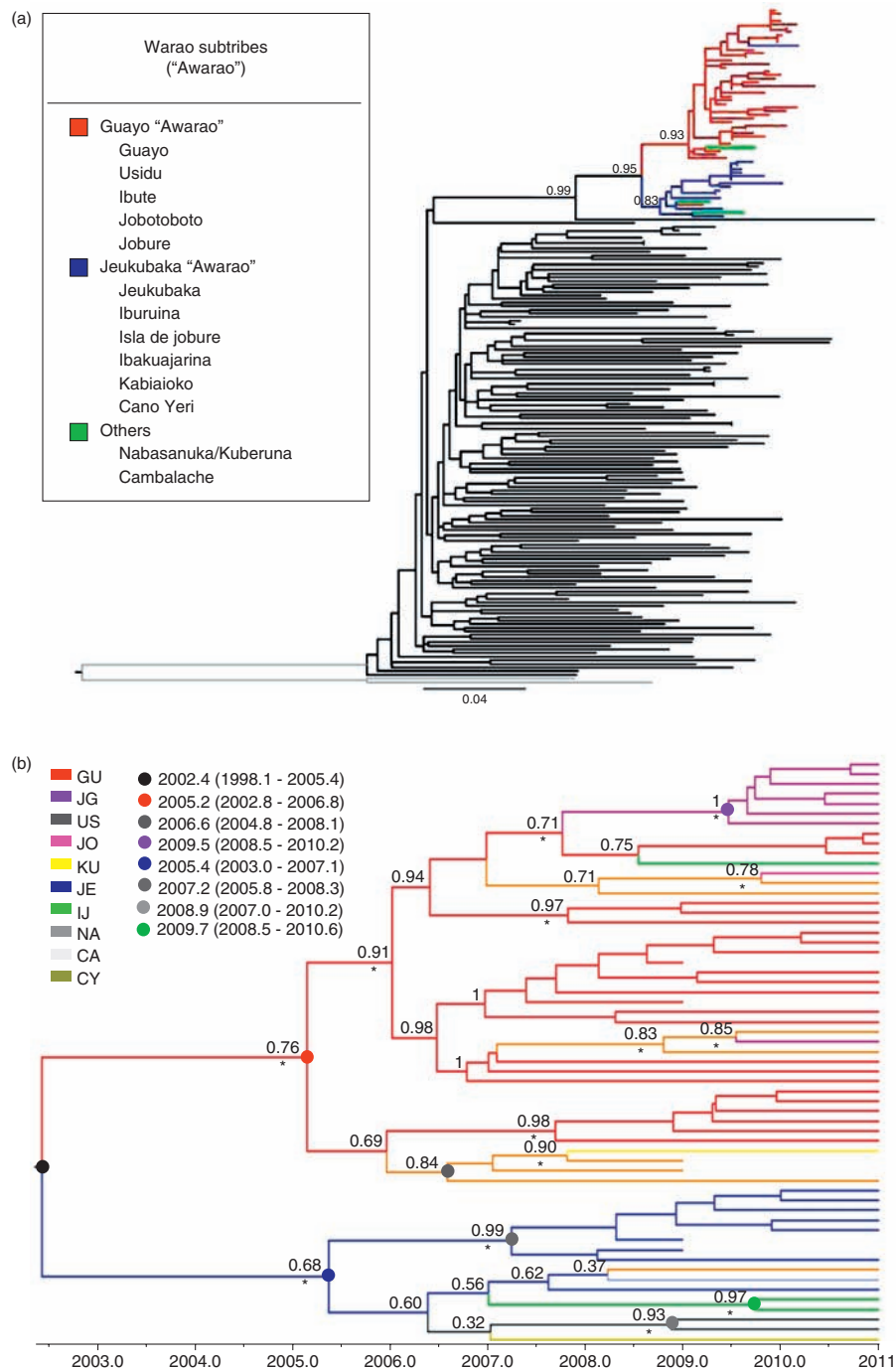


Fig. 2. Phylogenetic analysis of HIV-1 isolates infecting Waraos. (a) Maximum likelihood phylogenetic tree based on 186 HIV-1 subtype B pol (~1,400 pb) sequences from Venezuela. HIV-1 subtype B sequences infecting different Waraos communities are shown in colors according to the legend given in the figure. Sequences from other Venezuelan localities are shown in black. The *aLRT* support values are indicated only at key nodes. The tree was rooted using subtype C reference strains (grey branches) as outgroup. Horizontal branch lengths are drawn to scale with the bar at the bottom indicating nucleotide substitutions per site. (b) Time-scaled Bayesian MCC tree of the Warao HIV-1 subtype B clade. Branches are colored according to the most probable location state of their descendent nodes. The legend for the colors is shown on the left. The *PSP* (posterior state probability) of key nodes is indicated by numbers. Asterisks point to key nodes with a high *PP* (posterior probability) support (>0.95). The median T_{mrcs} (with 95% HPD interval in parentheses) of the Warao clade and other specific sub-clades marked by circles is shown on the left. Horizontal branch lengths are drawn to scale with the bar at the bottom indicating years. The tree was automatically rooted under the assumption of a relaxed molecular clock. San Francisco de Guayo, Jobure de Guayo (JG), Usidu (US), Jobotoboto (JO), Kuberuna (KU), Jeukubaka (JE), Isla de Jobure (IJ), Nabasanuka (NA), Cambalache (CA), and Caño Yeri (CY).

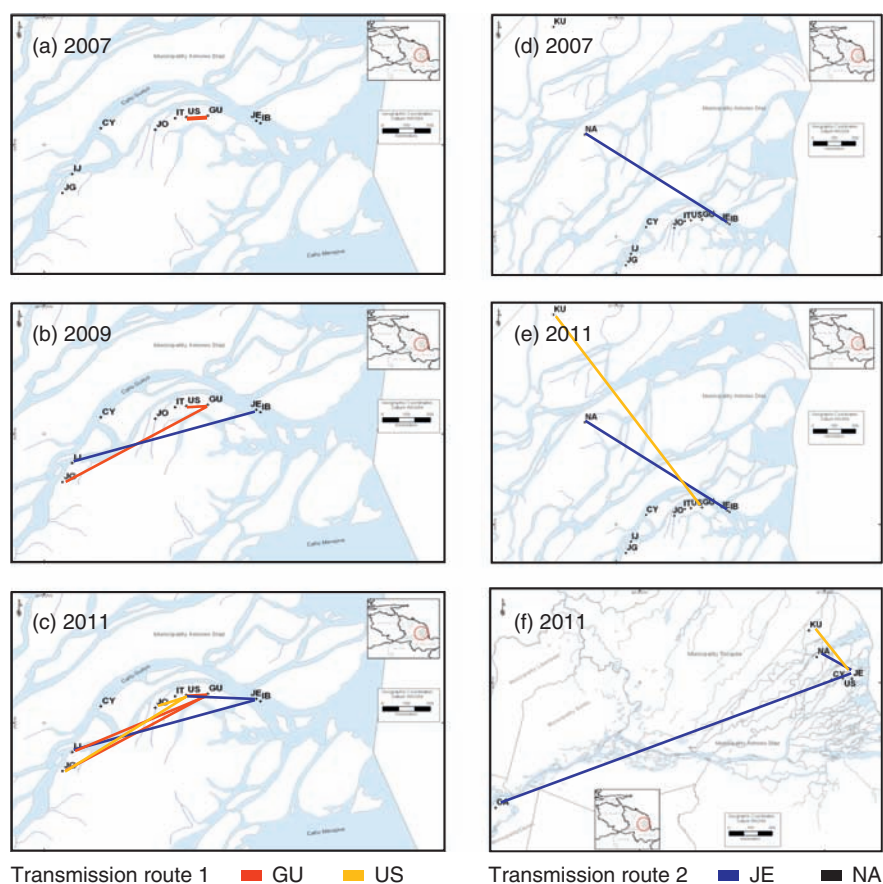


Fig. 3. Spatiotemporal dynamic of HIV-1 subtype B dissemination in Warao communities. We provide snapshots of the short (a–c), medium (d and e) and long (f) distances viral migrations events for the years 2007, 2009 and 2011. Lines between locations represent branches in the Bayesian MCC tree along which location transitions occurs. The colored lines represent the communities of source according to the legend at the bottom. San Francisco de Guayo, Jobure de Guayo (JG), Ibuiruina (IB), Jeukubaka (JE), Ibute (IT), Jobotoboto (JO), Usidu (US) and Isla de Jobure (IJ), Kuberuna (KU), Nabasanuka (NA), Cambalache (CA), and Caño Yeri (CY).

least two independent introductions of HIV-1 occurred in this tribe, one of subtype B, successfully established in the community, and another of subtype C infecting only one individual [8]. We extended this previous work through the analysis of a much larger sample of HIV-positive Warao individuals. We found no evidence of additional HIV-1 introductions in Waraos and we also confirmed that only subtype B was successfully disseminated in this population.

In approximately a decade, 9.55% of the population has been infected and a significantly higher HIV-1 prevalence was found among men (15.6%) than among women (2.6%). Although Warao people have been reported as monogamous and live in single-family dwellings [29], such difference could be explained by the homosexual and bisexual practices documented among Warao Amerindians [14]. It is common to find male-to-female transgender individuals (called 'tidawina' in Warao language) in some communities who maintain sexual practices with men on a daily basis [26]. Some anthropologists suggested that transgendered people

often used to be secondary 'wives' in polygamous marriages, therefore, having a more-or-less exclusive relationship (Allard O, personal communication). Three HIV-infected men included in our study were 'tidawina' individuals, although another five reported sexual intercourse with 'tidawinas' during menstruation of their wives, revealing the importance of homosexual practices for HIV dissemination in Warao communities. Additional anthropologic studies are needed to confirm this issue. In addition, three HIV-positive males were found to have serologically discordant female partners, despite reporting more than 3 years of continuous sexual activity with their mates. Further studies are needed to analyze the molecular mechanisms involved in an eventual protection to HIV-1 in some Warao women. As expected for a recent epidemic, young adults (18–30 years) were significantly more affected than persons from other age groups, the infection being frequently found in the working-age and more sexually active population.

Lack of knowledge about HIV and mystical beliefs about disease could be major risk factors for infection. More

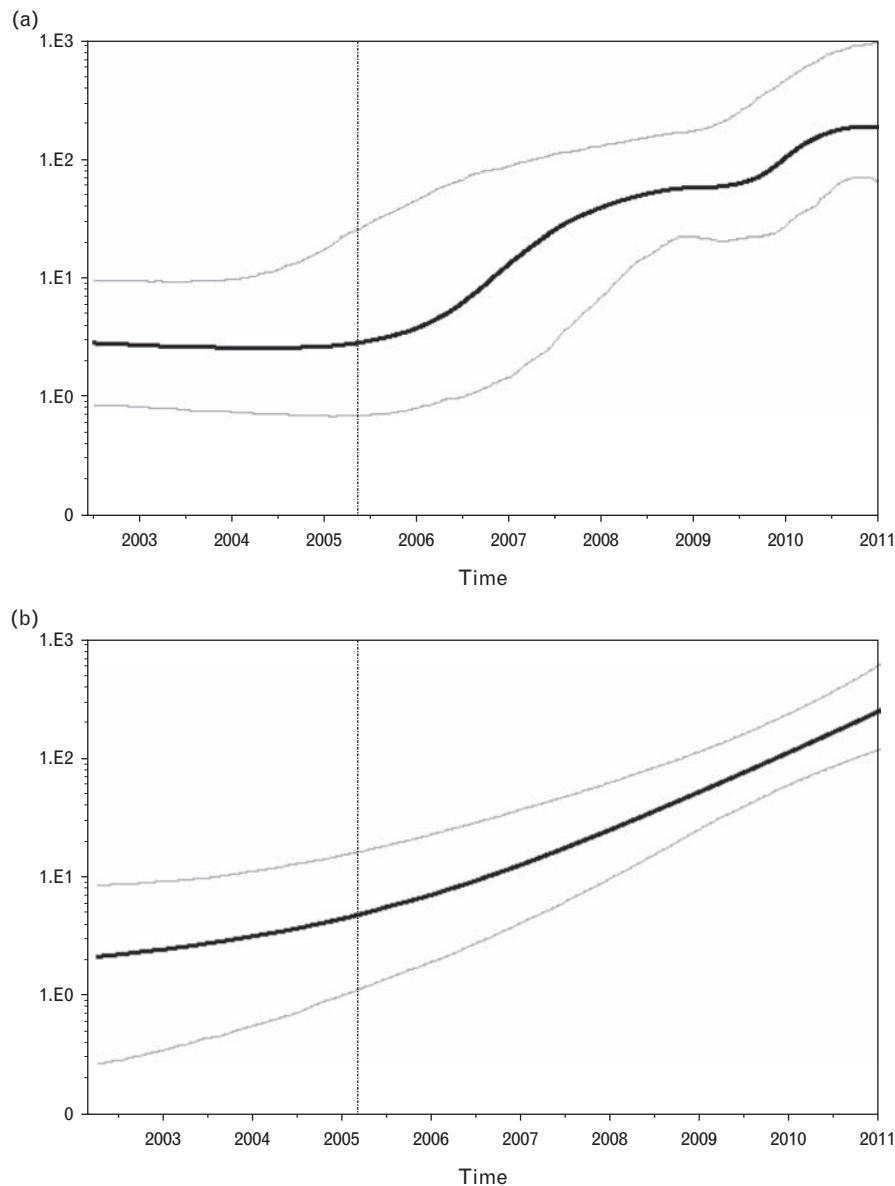


Fig. 4. Demographic history of the Warao HIV-1 subtype B clade. Graphics depict the median estimate (black line), and the 95% confidence limits (grey lines), of the effective number of infections (y-axis; log10 scale) through time (x-axis; calendar years) obtained using the Bayesian skyline plot (a) and the expansion growth (b) coalescent models. Dashed vertical line indicates the transition between the slow and the fast growth phases. The median estimated growth rate (with 95% HPD interval in parentheses) under the expansion growth model is shown on graph B.

than half of our patients were analphabets, reported no knowledge about HIV/AIDS before and had no experience in barrier methods. Moreover, some villagers from Usidu believe that after blood extraction, an evil spirit can enter their body and kill them some years later. Some neighbors have also rejected AIDS sufferers from their communities (Villalba J, personal communication). In addition, promiscuity and early sexual initiation were frequently reported, in contrast to previous anthropologic descriptions [27]. In this study, the mean number of sexual partners per individual was 4/year; with some patients reporting up to 30 partners/year. Young age of sexual

initiation in the HIV-positive patients was frequently reported. We also documented paid-sex, especially in the 'tidawina' individuals here included. Finally, the presence of one vertical case in our study group and other two mother-to-child transmission cases identified in the Merejina community by our group reveals that HIV surveillance of pregnant women in the Warao community is not adequate.

The phylodynamic analysis suggests that the HIV-1 subtype B was introduced in the Waraos at around the early 2000s. The median T_{mrca} was estimated in this study

as 2002, 3 years later than the one estimated in our previous study [8]. This difference could not be considered significant because the great overlap of the 95% HPD interval of both estimates (1998–2003) and can be attributed to a more precise estimation due to the higher number of sequences available for this study. After an initial phase of slow growth, the virus reached the Guayo and Jeukubaka communities at around 2005 and started to spread exponentially, following two major migratory routes. One route mainly comprises individuals from Guayo, Usidu and Jobure de Guayo and the other one mainly contains individuals from Jeukubaka. The gradient of HIV-1 prevalence found in Warao communities is fully compatible with the genetic history of viral dissemination, being the communities exhibiting the highest prevalence (Guayo, Jeukubaka and Usidu) the ones most anciently exposed to the virus. Moreover, the presence of two major transmission networks showed almost perfect agreement with the original practice of the Waraos to maintain relationships within endogamous subtribes ('awarao' in Warao language) [27,28]. The absence of HIV-1 cases in two communities, Iburuina and Ibute, might also be explained by the low rate of sexual intercourse with individuals from other subtribes (Warao-daïsa or hotarao in Warao language). These transmission patterns could be very useful for the implementation of programs to stop the spread of the epidemic to other subregions of the Orinoco Delta.

We previously found that the Warao clade share a distant relatedness with a sequence from a Venezuelan patient who lives in a distant populated city called Maracay [8]; suggesting that the Warao epidemic could have a distant origin in urban localities of Venezuela. The estimated origin of the HIV epidemic in the Waraos is posterior to a cholera epidemic (1993) during which many Warao individuals migrated to urban areas of Ciudad Guayana, San Felix, Barrancas, and Tucupita, where they founded slums in an accelerated acculturation process [15,28]. Of note, one HIV-1 isolate that branched within the Warao clade was from Cambalache, a distant community located 260 km away by river from the study area, in the proximity of a dump in Ciudad Guayana. Cambalache represents a community with great risk of HIV-1 infection due to prostitution and drug trafficking, and also hosts a population of about 150 Warao who live there permanently in miserable conditions as panhandlers (Villalba J, personal communication), of which 16 HIV-positive individuals have already been identified (Von Zeeland G, personal communication). More important, 53% of the HIV-1-infected Warao individuals here analyzed reported to have visited that community. Thus, we speculate that Cambalache might have played a role in the introduction or dissemination of HIV-1 in Waraos.

According to our estimations the HIV-1 subtype B spread in the Waraos with a median growth rate of around

0.81/year between 2005 and 2012. Notably, this growth rate is remarkably similar to that estimated for subtype B in both the general population from USA (0.83/year) [29] and within defined transmission clusters of MSM from United Kingdom (0.80/year) [30]. Our demographic reconstruction also suggests that the subtype B epidemic in the Warao communities is still growing and almost doubled its size in each year since 2005, which can be particularly devastating for this Amerindian community. HIV-1 patients from other geographical areas in the LOD such as Kuberuna, Siawani, Nabasanuka, Merejina, Cano Yeri, Ibakuajarina, Kabiajoko, San José de Amacuro and Curiapo, have already been identified, and drug-resistant strains are already transmitted among them [8]. Implementation of treatment schemes warrants further concern, as the Warao experience of chronic treatments is limited only to 6 months of TB treatment [28], and 12 HIV-1-positive patients referred seminomadism.

This multidisciplinary study raises the issue that Warao's HIV-1 epidemic is probably the result of a complex combination of traditional practices and external influences that has led to a profound loss of cultural identity in them. The Orinoco Delta is a vast territory in which implementation of public health policies to control the HIV epidemic and other infectious diseases faces singular constraints and requires far more epidemiologic data. This study provides an important framework for the design of adequate health interventions and highlights the need for an urgent and feasible medical-anthropological approach to stop HIV transmission in this population.

Conclusion

A dramatic high HIV-1 prevalence was documented in almost all of the studied communities of Warao Amerindians from the Orinoco Delta. This epidemic resulted from the dissemination of a single HIV-1 subtype B founder strain introduced about 10 years ago and its size is probably doubling at every year, creating a situation that can be devastating for this vulnerable Amerindian group, with a high prevalence of tuberculosis, hepatitis B, among other infectious diseases, and with limited access to primary healthcare.

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Conflicts of interest

There are no conflicts of interest

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