



# Mid and Late Holocene population changes at the Sabana de Bogotá (Northern South America) inferred from skeletal morphology and radiocarbon chronology

Miguel Eduardo Delgado Burbano <sup>a,b</sup>

<sup>a</sup>División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n. (B1900FWA), La Plata, República Argentina  
<sup>b</sup>Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), República Argentina

## ARTICLE INFO

### Article history:

Available online 30 October 2011

## ABSTRACT

The human history of the Sabana de Bogotá (SB) in Northern South America has been interpreted both as a continuous process of biocultural evolution and as a process of population discontinuities. Both hypotheses were evaluated on the basis of craniofacial morphology and radiocarbon evidence within a paleoenvironmental framework. The results suggest that the craniofacial morphology changed significantly over time. The investigation of the available radiocarbon database shows that there are hiatuses throughout the Holocene with a major gap between 4700 and 4100 <sup>14</sup>C BP, which is coincident with strong paleoenvironmental shifts. According to these results, a Population Discontinuity Model is presented which states that during the mid-Holocene (ca. 6000–3800 <sup>14</sup>C BP) population events as contraction/extinction and/or expansion/dispersals processes influenced by paleoenvironmental changes, promoted the almost complete depopulation of the SB, subsequently allowing the arrival of new hunter-gatherer populations from the Middle Magdalena Valley. Between ca. 2000–1500 <sup>14</sup>C BP, population expansions of agricultural societies from the east-northeast and/or from the Middle Magdalena Valley penetrated the SB and replaced the Herrera populations. The discontinuity scenario presented is compatible with the concepts of human biogeography and evolutionary geography.

© 2011 Elsevier Ltd and INQUA. All rights reserved.

## 1. Introduction

Since the 1970s, several authors have suggested that specialized hunter-gatherers penetrated the Sabana de Bogotá (SB), in Northern South America, during the late Pleistocene (ca. 13,000 <sup>14</sup>C BP) and remained without major population, technological and economical shifts until the arrival of foreign agriculturalists during the late Holocene (ca. 2500 <sup>14</sup>C BP) (Correal and van der Hammen, 1977; Correal, 1990; Neves et al., 2007) or even until the arrival of Spaniards in the 16th century (Rodríguez, 2007). According to this hypothesis, named here the Local Evolution Model (LEM), the archaeological record shows that the Abriense lithic industry persisted from the final Pleistocene until the late Holocene. Using stable isotope, paleobotanical and zooarchaeological data, a gradual change of the subsistence systems between ca. 10,000 and 2500 <sup>14</sup>C BP was suggested (Correal, 1990; van der Hammen et al., 1990). More recently, Correal (1990), Neves et al. (2007), and Rodríguez (2007) indicated that the cranial morphological patterns representing the same lineage suffered a gradual and subtle transformation throughout the Holocene. In

their view, the morphological patterns were affected neither by the arrival of foreign populations(s) nor by changes in the subsistence systems.

On the other side, some authors have presented some objections to the LEM. Dillehay (2000) detected, in a temporal sense, important cultural changes including a technological simplification of the stone tools and the inclusion of more plant and animal species in the diet. Nieuwenhuis (2002) identified significant shifts over time in the manufacture and use of lithic tools such as the appearance of more complex artifacts, the employment of foreign raw materials, the use of tools in non-specialized contexts and activities (i.e., broad-spectrum economies), and the increasing importance of wood working and vegetable resources. In addition, some authors have proposed population interactions since the late Pleistocene between the SB and the Middle Magdalena Valley, the Atlantic coast, the Middle Cauca and the Colombian southwest (Correal and van der Hammen, 1977; Nieuwenhuis, 2002; Aceituno and Loaiza, 2007; López, 2008). This dynamic scenario is incompatible with an *in situ* evolution model because population interactions promote cultural change, that is, induces cultural innovations and/or modifications. Gnecco (2000) and Nieuwenhuis (2002) suggested that the foreign raw material (chert from the Middle Magdalena Valley) found in El Abra, Tequendama, and Tibitó does not

E-mail address: [medelgado@fcnym.unlp.edu.ar](mailto:medelgado@fcnym.unlp.edu.ar).

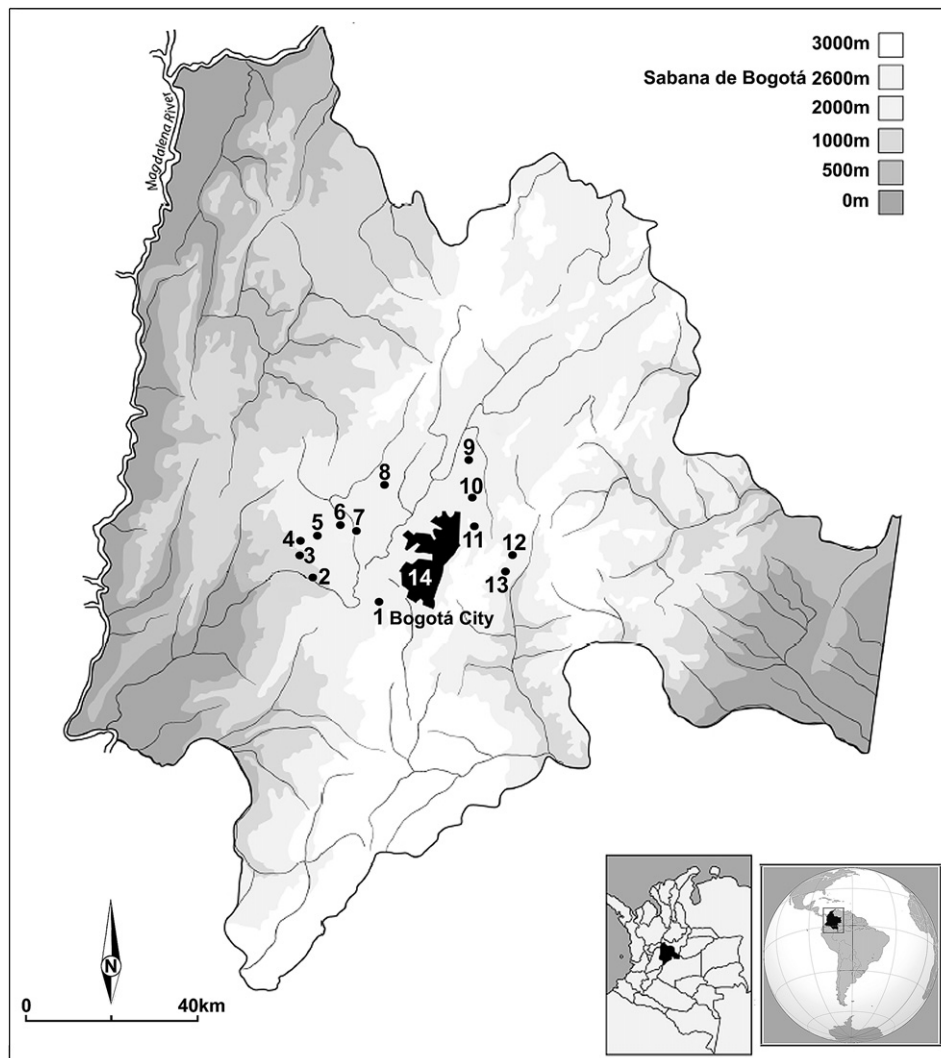
necessarily reflect territorial mobility, but rather intergroup contacts and/or economical exchange networks. Finally, Cárdenas (2002) through isotopic analyses criticized the specialized big game hunting model and stressed the importance of the use and consumption of vegetal resources, even since the early Holocene. This study also documented morphological differentiation throughout time.

Taking into account the two aforementioned positions regarding the Holocene human history of the SB, the aim of the present study is to evaluate both models using craniofacial morphology and radiocarbon evidence within a paleoenvironmental framework.

### 1.1. The area of study

The SB is a high plain located 2600 m asl on the eastern side of the Andean cordillera in Northwestern South America (Fig. 1). This high plain has an approximate area of 1400 km<sup>2</sup>, with slopes ranging between 3000 and 4000 m asl in the north and south side respectively (van der Hammen and González, 1960; Dueñas, 1980). In the region, the most important river is the Bogotá, although some lagoons exist. On the western side of the SB lies the

Magdalena River Valley, and on the eastern side the mountains slope down to the eastern plains. Geologically, the SB is a Neogene basin, product of a geological-evolutionary process whose last event was the raising of the basal sediments of Tilatá formation at the end of the Pliocene (van der Hammen and González, 1960; Dueñas, 1980). Throughout the Pleistocene and the Holocene, lake clays were deposited from the Sabana Formation which filled the basin, giving the cotemporary aspect of the SB (Dueñas, 1980; van der Hammen and Correal, 1992). At the present time this region supports an Andean forest characterized by the presence of *Weinmannia* sp. div., *Quercus* and other species (van der Hammen and González, 1960). There are no seasonal temperature fluctuations, only differences in rainfall, with wet seasons twice a year. The annual temperature lies between 12 and 18 °C and the annual rainfall varies between 500 and 1500 mm (van der Hammen and Correal, 1992). Regarding the faunal composition of the SB, the archaeological evidence suggests a high density of species including mammals (v.g. *Odocoileus virginianus*, *Mazama* sp., *Cavia porcellus*); reptiles (*Kinosternon postinginale*, *Crocodylia* sp.); fish (v.g. *Eremophilus mutisii*, *Pygidium bogotense*); birds (v.g. *Familia anatidae*, *Familia raliidae*) and crustaceous-gastropods (v.g. *Neostrengeria macropa*; *Drymaeus gratus*).



**Fig. 1.** The Sabana de Bogotá region showing the location of archaeological sites investigated (modified from Nieuwenhuis, 2002). 1 = Soacha; 2 = Tequendama; 3 = Aguazuque; 4 = Potreroalto; 5 = Vistahermosa; 6 = Bojacá; 7 = Galindo; 8 = Madrid; 9 = Nemocón; 10 = Checua; 11 = Chía III; 12 = Sueva; 13 = Guavio; 14 = Muisca settlements.

**Table 1**  
Samples of human cranial remains analyzed including chronological period and sample size.

Site/group name	Regional sample	Chronological period	Sample size
Sabana de Bogotá samples			
Final-late Holocene	Soacha, Marín, Portalegre, Candelaria, Bojacá, Las Delicias, Tunjuelito, Bogotá	Muisca period ca. 1500–400 <sup>14</sup> C BP	134
Initial-late Holocene	Aguazuque, Checua, Madrid, Mosquera, Tequendama, Zipacón	pre-Herrera period ca. 3500–2500 <sup>14</sup> C BP	33
Mid-Holocene	Aguazuque, Chía III	ca. 5000–3800 <sup>14</sup> C BP	44
Early-mid Holocene	Checua, Tequendama, Guavio <sup>a</sup> , Sueva <sup>b</sup> , Galindo, Potreroalto	ca. 8000–6000 <sup>14</sup> C BP	27
Samples from other Colombian Regions			
Caribbean	Trementina cave; Perijá, Sabana larga, Simtí; Guajira; Gamarra; Manaure, Turbaná	ca. 1000 <sup>14</sup> C BP	16
Guane	Santuario cave; Los Santos; North Santander Region	ca. 1325–300 <sup>14</sup> C BP	37
Panche-Lache	Agua de Dios; Tibacuy; Jericó	ca. 1840 <sup>14</sup> C BP -XVI century	29
Cauca river valley	Coronado; El Cerrito; Estadio; Guacarí, Malagana; Santa Bárbara	ca. 2950–2000 <sup>14</sup> C BP	33
Nariño (South Colombia)	Ancuyá; Boboná; Tajumbina; La Paloma; Marídiaz	ca. 1500 <sup>14</sup> C BP- XVII century	9
Total			362

<sup>a</sup> Associated date: 9360 ± 45 <sup>14</sup>C BP.

<sup>b</sup> Associated date: 10,090 ± 90 <sup>14</sup>C BP.

## 2. Materials and methods

### 2.1. Human skeletal remains investigated

The SB is one of the few archaeological regions in Northern South America where well preserved human skeletal remains for the last 10,000 <sup>14</sup>C BP are available. The skeletal evidence has been intensively used in the discussion of the early settlement of the Americas (for a synthesis see Neves et al., 2007; Rodríguez, 2007). Fourteen skeletal series representing 239 adult individuals of both sexes were studied (Table 1; Fig. 1). Four chronological groups were conformed in order to obtain a better picture of the morphological differentiation. These include early mid-Holocene (EMH ca. 8000–6000 <sup>14</sup>C BP); mid-Holocene (MH ca. 5000–3800 <sup>14</sup>C BP); initial-late Holocene (ILH ca. 3500–2500 <sup>14</sup>C BP) and final-late Holocene (FLH ca. 1500–400 <sup>14</sup>C BP). In addition, 123 individuals from other Colombian cultural areas were included to perform inter-regional comparisons (Table 1).

Thirty-two craniometric measurements (Table 2) were scored following the description set by Howells (1973). With the aim of enhancing the statistical analyses, different procedures were performed: a) only non-deformed skulls were analyzed; b) individuals with more than 40% of missing data were excluded; c) to estimate missing values a multiple imputation program named NORM 2.03 (Schafer, 1999), using a data augmentation algorithm, was employed; d) the original linear measurements for each individual were converted into Mosimann shape variables (Darroch and Mosimann, 1985); and e) shape variables were transformed to z-scores in order to minimize sex-related size differences. The inter-group comparisons were conducted employing two different approaches. The first one uses common statistical techniques to assess the degree of morphological affinity. These include discriminant analysis (DA), and Mahalanobis  $D^2$  generalized distance. Two-dimensional scatterplots were used to display graphically the intersample relationships. The second approach uses the Relethford and Blangero (1990) method of intraregional heterogeneity (R-matrix) to model the magnitude and direction of gene flow over time. Further details of this method are provided by Relethford and Blangero (1990). As this model requires population sizes to be known, a weight coefficient of 1 was set to early and mid-Holocene hunter-gatherers samples and a value of 2 was set to final-late Holocene agriculturalists. This implies that the last groups have a twofold population size. In this work, a heritability value equal to 1 was used. The phenotypic distances were obtained from the scaled- unbiased biological distance matrix ( $d_{ij}^2$ ) and graphically

displayed by plotting the eigenvectors of the first two principal coordinates. The analyses were performed using the program RMET 5.0 written by J. Relethford.

Lastly, matrix correlation analyses were used in order to evaluate competing hypothesis for the explanation of the morphological variation observed in the SB. Three simple design matrices (see below) were constructed taking into account the assumptions of two models about the population continuity (LEM) or discontinuity (PDM). In the first model (LEM), the four diachronic samples display non-significant distances ( $D^2$ ) because they are the same people evolving over time. Therefore all samples share a distance value of 0. In contrast, in the second model (PDM) all samples exhibit significant biological distances because they represent foreign

**Table 2**  
Thirty two craniometric measurements used in the present study<sup>a</sup>.

Measurement	Code
Glabello-occipital length	GOL
Nasio-occipital length	NOL
Basion-nasion length	BNL
Basion-bregma height	BBH
Maximum cranial breadth	XCB
Maximum frontal breadth	XFB
Bizygomatic breadth	ZYB
Biauricular breadth	AUB
Minimum cranial breadth	WCB
Biasterrionic breadth	ASB
Basion-prosthion length	BPL
Nasion-prosthion height	NPH
Nasal height	NLH
Nasal breadth	NLB
Palate breadth	MAB
Mastoid height	MDH
Mastoid width	MDB
Orbit height	OBH
Orbital breadth	OBW
Interorbital breadth	DKB
Bimaxillary breadth	ZMB
Bifrontal breadth	FMB
Biorbital breadth	EKB
Nasion-bregma cord	FRC
Bregma-lambda chord	PAC
Lambda-opisthion chord	OCC
Minimum frontal breadth	M9/WFB
Cheek height	WMH
Bijugal breadth	JUB
Malar length maximum	XML
Foramen magnum length	FOL
Foramen magnum breadth	FOB

<sup>a</sup> Measurement definitions in Howells (1973).

populations penetrating the SB in different moments of the Holocene. Under this assumption, all samples share a distance value of 1, except EMH–FLH and MH–FLH which share a distance value of 2 because they are the most temporally separated samples. Lastly, a temporal distance matrix was constructed (TEMPO). This model states that the morphological differentiation is a function of time. Therefore, early and mid-Holocene samples should be morphologically different from the late Holocene ones. The Mantel test was employed to evaluate the correlation between two matrices, and the Smouse–Long–Sokal test was used in order to include a third matrix in the model (v.g. temporal distance). Significance of the correlation was determined by a permutation test (9999 permutations).

## 2.2. Radiocarbon dates analyzed

Some authors have recently paid special attention to the radiocarbon dates as indicators of the level of archaeological signal, which can be influenced by several factors including population dynamics, changes in the spatial organization (i.e., differential density, mobility, etc) and those related to differential preservation of sites and archaeological sampling (Williams, 2011). Accordingly, the frequency of  $^{14}\text{C}$  dates is used to know past human activity, which despite some biases (Surovell and Brantingham, 2007), relatively reflects the intensity of human occupation at the regional level. In order to search for discontinuities in the dates sequence with population and regional significance (i.e., not exclusively influenced by taphonomic biases), a  $^{14}\text{C}$  database was constructed taking into account the available literature. The current database is composed of a minimum of 142 uncalibrated dates representing nearly 70 archaeological sites. The dating methods employed were beta-counting and AMS. However, nearly 90% of the dates were obtained through beta-counting. The materials used for dating were diverse, including bone collagen, charcoal, macro-botanical remains, sediments and gastropods. Given that charcoal was the preferred dating material, the association between occupation event-date should be seen with caution. For the chronological information analyzed here, different procedures were performed in order to enhance the quality of the data: a) dubious dates and/or considered problematic by the original authors of the reports were excluded of the analysis; b) some dates obtained on bone collagen through the beta-counting method were corrected for isotopic fractionation. A mean value of  $-20.1\text{‰}$  ( $\delta^{13}\text{C}$ ) obtained from an assemblage of human archaeological bone from the SB region was used for correction; c) the magnitude of the measurement error (i.e., laboratory uncertainty) was assessed, and those dates with high sigma values ( $1\sigma > 250$  years) were rejected; d) some outliers, those corresponding to early dates that exceeded the most accepted date for the initial peopling of the region ( $12,400 \pm 160$   $^{14}\text{C}$  BP) were deleted from the database; and e) some dates belonging to the same site and occupation level were pooled evaluating their statistical similarity ( $\chi^2$ ,  $p < 0.05$ ) using the module test sample significance in the program CALIB 6.01 (Stuiver et al., 2005). This filtering process produced a final dataset integrated by 100 radiocarbon dates covering  $\sim 12,400$   $^{14}\text{C}$  BP ( $\sim 14,000$  cal BP). One of the main goals of the present study, with compiled published  $^{14}\text{C}$ -data from Late Pleistocene and Holocene sites from the SB region, was to establish a radiometric chronology on the numerical time scale, which can be directly compared with available high-resolution paleoclimate records. Accordingly, the  $^{14}\text{C}$  ages were calibrated with the CalPal-software (Weninger and Jöris, 2004), using the CalPal-2007-Hulu  $^{14}\text{C}$ -age calibration curve (Weninger and Jöris, 2008). The CalPal-package, from a basically explorative-graphic approach, allows simultaneously  $^{14}\text{C}$ -age calibration and its comparison with paleoclimate proxies displayed on a compatible (calendaric) time scale

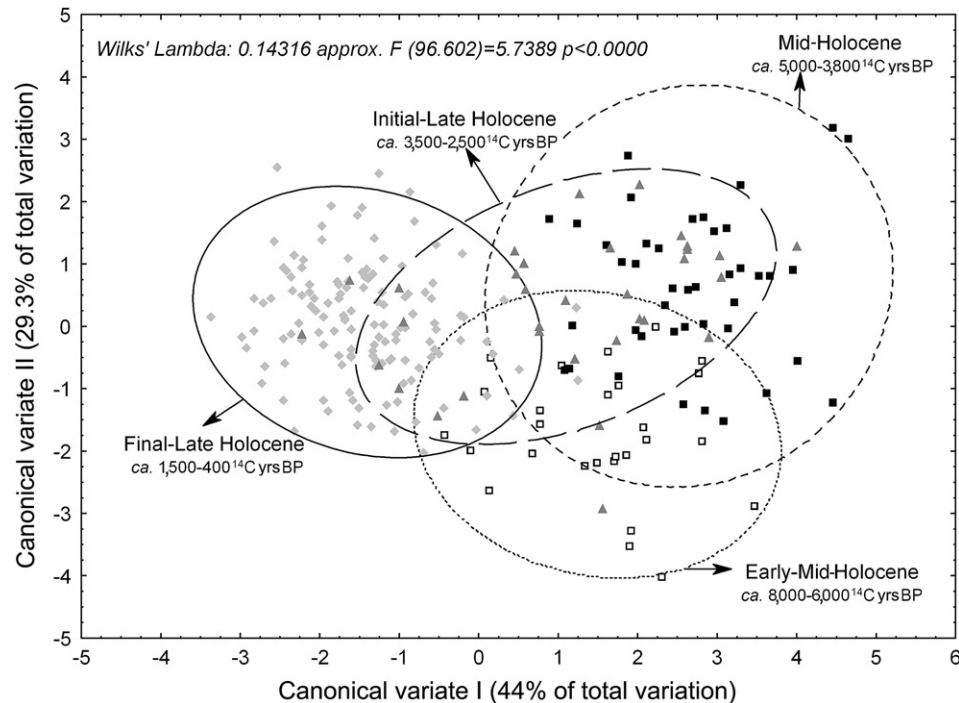
(Weninger and Jöris, 2004). The resulted summed calibrated probability of  $^{14}\text{C}$ -age distribution is a 2-D graph that shows both the probability distribution ( $2\sigma$ ) of the  $^{14}\text{C}$ -ages and selected paleoclimate proxies on the calendaric time scale (Weninger and Jöris, 2004). In this study, the calibrated  $^{14}\text{C}$ -ages were compared with two paleoclimate proxies: the Cariaco Basin varve series (Hughen et al., 1998), and the Sajama icecap (Thompson et al., 1998). Such proxies (paleotemperature curves) were included given their regional and hemispheric significance and because are reliable indicators of paleoclimatic change within the South American tropics. Finally, the chronological position of four of the six periods of rapid climatic change (RCC) globally identified by Mayewski et al. (2004), is indicated. This exploratory procedure permits a more detailed view of the possible influence of specific Holocene climatic pulses on regional population dynamics. The RCC included are: RCC1 9000–8000 cal BP; RCC2 6000–5000 cal BP; RCC3 4200–3800 cal BP and RCC4 3500–2500 cal BP.

## 3. Results

### 3.1. Craniofacial evidence

The results of the discriminant analysis indicate the existence of significant differences between all samples: Wilks' Lambda: 0.14316 approx.  $F(96.602) = 5.7389$   $p < 0.0000$ . In Fig. 2 are plotted the first two canonical variables, which show morphological differentiation following a diachronic trend, that is, late samples are morphologically different from early samples. The computation of the  $D^2$  distances between pairs of SB samples indicates that all are statistically different.  $F$ -values =  $32.2^\circ$  of freedom, EMH vs. MH = 7.1 ( $F = 3.2$ ;  $p < 0.0001$ ); EMH vs. ILH = 6.0 ( $F = 2.3$ ;  $p < 0.0001$ ); EMH vs. FLH = 11.6 ( $F = 7.0$ ;  $p < 0.0001$ ); MH vs. ILH = 5.5 ( $F = 2.7$ ;  $p < 0.05$ ); MH vs. FLH = 16.8 ( $F = 14.6$ ;  $p < 0.0001$ ); ILH vs. FLH = 8.0 ( $F = 5.7$ ;  $p < 0.0001$ ). The R-matrix analysis (Fig. 3 and Tables 3 and 4) also shows deep morphological differences among the diachronic samples. In Fig. 3, a scatterplot representing the minimum population distances is shown. The four diachronic samples are quite different, although the MH and ILH groups are the less differentiated. In Table 3, the computation of minimum  $F_{ST}$  values for different subsets of data according to several comparison criteria is presented. Minimum  $F_{ST}$  among all SB diachronic samples is 0.032. Minimum  $F_{ST}$  for the early-mid and mid-Holocene samples is 0.036 and for initial-late Holocene and final-late Holocene is 0.019. This indicates that the levels of gene flow during the early and mid-Holocene were greater than during the late Holocene. This finding is corroborated through the analysis of differential gene flow (Table 4). According to these results, the early-mid Holocene, mid-Holocene and initial-late Holocene samples have greater than expected within-group phenotypic variance, but the final-late Holocene group has lower than expected. When the SB is compared to other regions, the minimum  $F_{ST}$  values become greater. In Table 5 the pairwise hypothesized distances according to two different models of population continuity/discontinuity, including the temporal distance and the computed biological ( $D^2$ ) distance are indicated. Results of matrix correlation analysis are presented in Table 6. Remarkable in this table is the high correlation between biological  $D^2$  and temporal distance ( $r_{D2,TEMPO} = 0.817$ ;  $p < 0.001$ ). This means that the differences observed in craniofacial morphology in the SB are related to temporal distance (i.e., the increase of gene flow over time). The most important result is the high and significant correlation between the biodistance matrix and the PDM scenario ( $r_{D2,PDM} = 0.902$ ;  $p < 0.001$ ). When the biological distance matrix was compared to the designed models, holding TEMPO constant, (Table 7) the partial correlation between biodistance and PDM still is high and statistically significant ( $r_{D2,PDM} = 0.675$ ;  $p < 0.001$ ). In



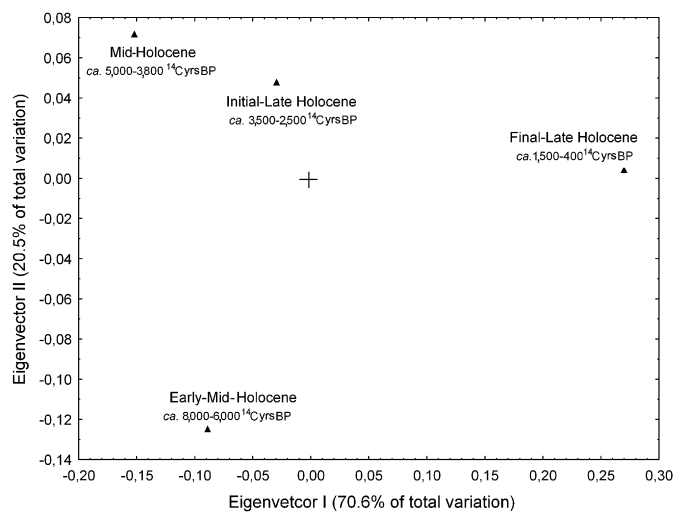


**Fig. 2.** Scatterplot of the first two canonical variables (73.3% of total variation) obtained from the discriminant analysis of 32 craniofacial measurements from four Sabana de Bogotá diachronic samples.

general terms these results indicate that temporal differentiation and a model (PDM) considering multiple population discontinuities better fits to the patterns of craniometric variation.

### 3.2. $^{14}\text{C}$ calibrated dates within a paleoenvironmental framework

In Fig. 4, the climatic and vegetation evolution including biome reconstructions for the SB and surrounding areas for the last 19,000  $^{14}\text{C}$  years on the basis of palynological, glaciomorphological and diatom evidence is presented (Marchant et al., 2002; Vélez et al., 2006; Gómez et al., 2007). The chronological position of the Guantiva interstadial and the El Abra stadial which are the regional



**Fig. 3.** Scatterplot of the first two eigenvectors (93.2% of the total variation) based on the scaled unbiased biological distance matrix ( $d_{ij}^2$ ) showing the minimum population distances among four diachronic samples from the Sabana de Bogotá region. Each axis has been scaled by the square root of its corresponding eigenvalue.

equivalents of the European Böllin-Allerød interstadial and the Younger Dryas Chronozone (YDC) (van der Hammen and Hooghiemstra, 1995) is indicated. In addition, the approximate chronological position of the mid-Holocene climatic optimum is also showed. In Fig. 5 a 2-D plot of the summed probability distribution of  $^{14}\text{C}$ -ages on the calendaric time scale (14,000–500 cal BP) of 100 radiocarbon dates, including the positions of YDC and the four RCCs and the paleoclimate proxies compared is presented. The pattern shows a punctuated peopling with an uneven archaeological signal, confirming previous analyses performed upon calibrated and uncalibrated dates in the Northern Andean Area (Delgado Burbano et al., in press). Basically three main clusters of  $^{14}\text{C}$ -ages are evident, all separated by gaps of different lengths. Contrary to previous suggestions, this pattern likely indicates a discontinuous peopling dynamic at the regional level.

The initial occupation of the region occurred during the last glaciation (i.e., Guantiva interstadial), ca. 14,817–12,914 cal BP (Fig. 5). For this period, pollen records from the lake Fúquene, the Guantiva páramo, the El Abra Valley and Pantano de Vargas suggest a warm period with very similar present-day temperatures ( $2^\circ\text{C}$

**Table 3**

Minimum  $F_{ST}$  values for craniometric traits calculated for several arrays of the total set of populations.

Samples included	Minimum unbiased $F_{ST}$	Standard error
All Sabana de Bogotá samples	0.032	0.003
Early-Mid Holocene – Mid-Holocene	0.036	0.006
Initial Late Holocene – Final Late Holocene	0.019	0.003
Sabana de Bogotá samples + neighboring region samples (Panche, Lache, Guane)	0.037	0.003
Sabana de Bogotá samples + other Colombian regions (Caribbean, Nariño and Cauca river Valley)	0.063	0.006
Other Colombian regions (Caribbean, Nariño and Cauca river Valley)	0.087	0.011
All samples	0.056	0.004

**Table 4**

Analysis of differential gene flow in the Sabana de Bogotá region during the Holocene<sup>a</sup>.

Sample	Distances to the centroid (rii)	Observed variance	Expected variance	Residual variance
Final-late Holocene	0.0473	0.734	0.939	-0.205
Initial-late Holocene	0.0589	1.149	0.985	0.164
Mid-Holocene	0.0563	0.992	0.930	0.062
Early-mid Holocene	0.0400	0.967	0.946	0.021

<sup>a</sup>  $F_{ST} = 0.032$ ; Standard Error = 0.003.

lower than today) (van der Hammen and González, 1960). An expansion of the forest (i.e., *Alnus*) and marsh vegetation (*Myrica* and *Symplocos*) occurred as well. Pollen-based biome reconstructions (Fig. 4) reveal environmental conditions relatively similar to those of LGM period, although with an increased spread of cool evergreen forest biomes at mid altitudes, thus revealing some climatic amelioration (Marchant et al., 2002). At the El Abra stadial (ca. 12,914–11,795/10,864 cal BP) the climate was very cold again with temperatures ranging between 6 °C and 4 °C lower than today. The forest partially disappeared and was replaced by subpáramo low bushes (van der Hammen and González, 1960). Biome reconstructions (Fig. 4) reveal that during this initial occupation phase there was a dominance of the cool grassland–shrub biome (Marchant et al., 2002). During this period, characterized by significant climatic and ecological changes a progressive increase in the archaeological signal is evident (Fig. 5). On the other hand, the intensity of the archaeological signal during the initial early Holocene is lower and coincident with a minor gap between ca. 9000–8700 cal BP (Fig. 5), which coincides with the RCC1, the “Glacial Aftermath” RCC (9000–8000 cal BP). During this same time span at least one of the two proxies compared (i.e., Cariaco varves) highly fluctuated (Fig. 5). The biome reconstructions for the 9500–8500 <sup>14</sup>C BP (ca. 10,800–9500 cal BP) interval reveal that there was a notable expansion of mesic biomes (Fig. 4). At higher elevations, cool mixed forest spread at the expense of the cool grassland–shrub biome. According to Marchant et al. (2002) this interval was clearly characterized by warmer and wetter conditions than those of the last part of the Lateglacial.

After 8600 cal BP until 5600 cal BP, a new period of occupation is evident (Fig. 5). The paleoenvironmental records show vegetation changes, increase and decrease of precipitations and temperature (i.e., annual temperature average) with a tendency to a dry environment and the subsequent decrease of water flow (Fig. 4) (Vélez et al., 2006; Gómez et al., 2007). The probability distribution of calibrated <sup>14</sup>C-ages also shows a fluctuating but continuous archaeological signal with a decline for the final period of this interval. During this period the two proxies compared also indicate temperature instability suggesting changes in the climatic conditions. According to some paleoecological studies (van der Hammen and González, 1960; Gómez et al., 2007), there were pulses of humidity and dryness throughout the interval. The Fig. 5 shows

**Table 5**

Pairwise hypothesized distances according to two models of population continuity/discontinuity for the Sabana de Bogotá during the Holocene, including temporal distance and computed biological ( $D^2$ ) distance<sup>a</sup>.

Population	LEM	PDM	TEMPO	$D^2$
EMH–MH	0	1	0	7.1
EMH–ILH	0	1	1	6.0
EMH–FLH	0	2	2	11.6
MH–ILH	0	2	0	5.5
MH–FLH	0	1	2	16.8
ILH–FLH	0	1	0	8.0

<sup>a</sup>  $F$ -values = 32.2 degrees of freedom; LEM = Local Evolution Model; PDM = Population Discontinuity Model; TEMPO = temporal distance.

**Table 6**

Correlations between one biological, one temporal and two design distance matrices.

	$D^2$	TEMPO	LEM	PDM
$D^2$	0			
TEMPO	0.817**	0		
LEM	-0.752 ns	-0.816 ns	0	
PDM	0.902**	0.866**	-0.707 ns	0

\*\* $p < 0.001$ ; ns = not significant; LEM = Local Evolution Model; PDM = Population Discontinuity Model; TEMPO = temporal distance.

that during the humid period there is a relatively high signal between 8660 and 7200 cal BP and a low signal during the dry period between 7000 and 5600 cal BP.

Between approximately 5400 and 4600 cal BP, there is a significant gap in the curve of <sup>14</sup>C calibrated dates (Fig. 5). According to the paleoenvironmental record during the mid-Holocene ca. 6000–4000 cal BP there was an increase in temperature ( $\pm 2$  °C) and a decrease in precipitation, which caused a particular dry period (Fig. 4). Data from Páramo de Palacio, Fúquene lake and Duitama high plain shows an alternation between *Alnus*-dominated swamp forest and open grassy vegetation, reflecting fluctuating water levels (Gómez et al., 2007). Actually, the last authors indicated that warmer and drier conditions between 6503 and 3880 cal BP also were detected at Turbera los Calostros, Páramo de Chingaza, Páramo Peña Negra and at Laguna de la América (3650 m asl). Fig. 4 also shows that during the mid-Holocene climatic optimum (7000–5000 <sup>14</sup>C BP) until ca. 3500 <sup>14</sup>C BP, the pollen and lacustrine indicators reflects low lake levels and lesser precipitations suggesting a warm and dry period. According to some archaeological and palaeoecological studies these conditions suggest a decline of the human presence in the SB, indicating possibly population dispersals (Correal and van der Hammen, 1977; Ardila, 1984; Correal, 1990). Ardila (1984:13); Correal and van der Hammen (1977:184–188) and van der Hammen and Correal (1992:225) state that the indicators of vegetation history in the SB show that the warm-dry mid-Holocene climate could cause water scarcity and the disappearance and/or contraction of open marshy and forest hunting areas. In some sites (v.g. Tequedama, El Abra, Checua) the considerable decline of faunal remains and artifacts reveals that the region was less occupied by humans during this period. The Fig. 5 shows that both proxies have high peaks during this period. Additionally, the RCC2 (ca. 6000–5000 cal BP) also is partially coincident with this interval of null archaeological signal, which according to Mayewski et al. (2004) is probably the result of roughly synchronous changes in the global hydrological cycle and in the solar radiation.

Finally, after the mid-Holocene gap, the archaeological signal has a progressive increase, with highest peaks between the 2300 and 500 cal BP, revealing a period of intense regional occupation (Fig. 5). Additional minor gaps (4600–4100 cal BP; 4000–3700 cal BP; 2800–2400 cal BP) were detected, some synchronized with the third and fourth RCC (cool poles/dry tropics) also associated with

**Table 7**

Partial correlations between one biological distance and two models, holding TEMPO constant.

Model	$D^2$
LEM	-0.254 ns
PDM	0.675**

\*\* $p < 0.001$ ; ns = not significant; LEM = Local Evolution Model; PDM = Population Discontinuity Model; TEMPO = temporal distance.

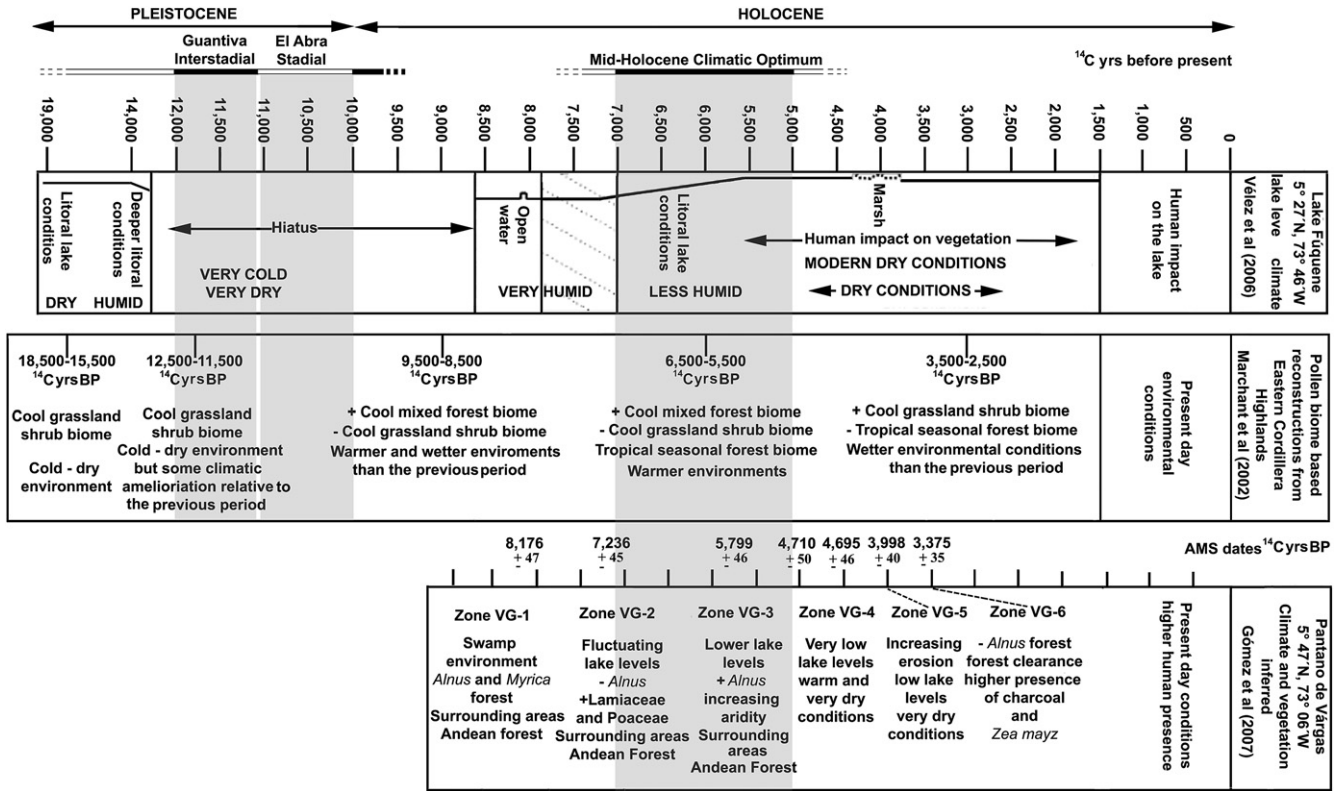


Fig. 4. Climatic-vegetation evolution and biome reconstructions for the Sabana de Bogotá region and surrounding areas for the last 19,000 <sup>14</sup>C yrs on the basis of palynological, glaciomorphological and diatom evidence. Zone VG = each Pantano de Vargas pollen zone. The grey bars show the chronological position of the Quantiva interstadial, El Abra stadial and the mid-Holocene climatic optimum.

solar variability and dryness (Mayewski et al., 2004). After the 2400 cal BP the climatic conditions became similar to today and the high precipitation (reflected by the increase of marshy herbaceous vegetation and open water) allowed an increase of the resource availability (carrying capacity) in the SB (Fig. 4). The pollen and sediment records also suggest intensive occupation reflected in

deforestation (*Quercus* in particular); lowering of water tables and increasing disturbance, probably by erosion (presence of *Amaranthaceae/Chenopodiaceae*, *Borreria* and *Dodonaea*); crop cultivation (presence of *Zea mays*) and frequent fires (as shown by the high amounts of charcoal in the sediments) (Vélez et al., 2006; Gómez et al., 2007).

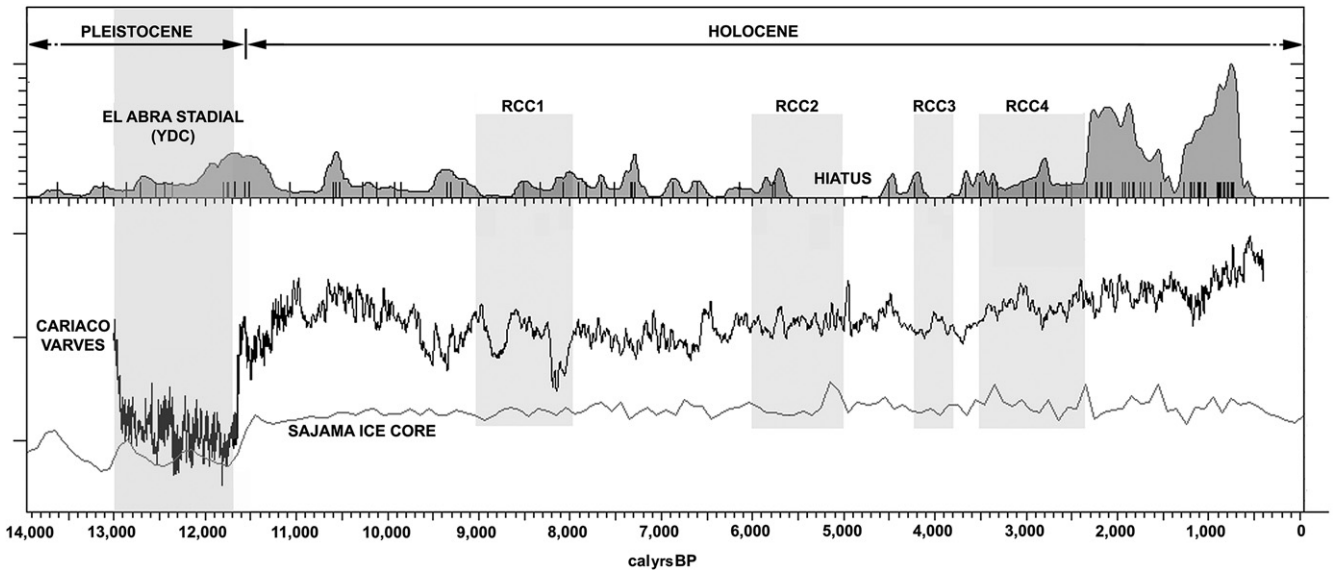


Fig. 5. (Top) Plot of the summed probabilities of the <sup>14</sup>C-ages on the calendaric time scale (14,000–500 cal BP) of 100 radiocarbon dates for the sample composed by archaeological sites from the Sabana de Bogotá region. The grey bars show the chronological position of the El Abra stadial or YDC and four periods of rapid climatic change (RCC) identified by Mayewski et al. (2004) in the Holocene. (Bottom) Temperature curves from two proxies, the Cariaco Basin varve series (southern Caribe), and the Sajama icecap (Central Andes).

#### 4. Discussion: towards a population discontinuity scenario for the human history of the Sabana de Bogotá

The different lines of evidence aforementioned suggest that between 6000 and 3800  $^{14}\text{C}$  BP and between 2000 and 1500  $^{14}\text{C}$  BP there were important population changes at the SB. The radio-carbon evidence indicates that during the mid-Holocene, between 4700 and 4100  $^{14}\text{C}$  BP (5400 and 4600 cal BP), a significant reduction in the archaeological signal (i.e., visibility) of the SB population occurred. This decrease in the archaeological visibility coincides with severe environmental changes including an increase in temperature ( $\pm 2$  °C) and aridity. Although this likely indicates that very few people remained in the SB during that period, it remains unclear if it is related to a population contraction (i.e., demographic declining), a local extinction and/or population dispersals. However, the morphological analyses strongly suggest that the early-Holocene group is significantly different to the mid-Holocene sample. In addition, the rates of gene flow during this same time span increased, suggesting that new populations probably entered the region. Thus, the mid-Holocene environmental fluctuations seem to be linked with a period of cultural change. Such fluctuations also may have had the potential to cause significant ecological modifications resulting from climate-dependent chorological changes affecting vegetal and animal communities. In this context, the zooarchaeological record shows that the remains of deer (*O. virginianus* and *Mazama* sp.), the main meat source in the region, progressively declines since ca. 8000–7000  $^{14}\text{C}$  BP with a remarkable reduction during the mid-Holocene (Correal and van der Hammen, 1977; Ijzereef, 1978; Cárdenas, 2002; Nieuwenhuis, 2002). It should be noted that the climatic warming can reduce mammalian fertility, leading to reduction in population numbers and, in abrupt climatic changes, collapse of mammalian populations (McLean, 1991). Therefore, it seems likely that the increase in temperature and aridity together with the relative lack of water caused on the one hand the retraction and/or disappearance of some areas (open and forest) used for hunting and the consecution of vegetal resources, and on the other hand the decline of deer populations. This has important population implications because according to evolutionary geography and human biogeography, past climate and ecological changes can promote contraction/extinction and expansion/dispersal processes depending of the population size and the mortality–survival equilibrium with the carrying capacity of the environment (Lahr and Foley, 1998). One of the most important determinants for the evolution of dispersal rates is the extinction risk to which local populations are exposed (Lahr and Foley, 1998). They result in empty or thinly populated patches, the existence of which makes dispersals both feasible and profitable (Barrientos and Pérez, 2005). In small hunter-gatherer groups, the mentioned phenomena could have higher effects on their population structure. In agreement with this setting, the lack of critical resources, together with adverse climatic and environmental conditions during the mid-Holocene increased the extinction risk, producing in turn, the dispersal and/or contraction (demographic and spatial) of most SB human populations. This likely allowed foreign populations to penetrate the thinly populated region. Several authors mention that during the mid-Holocene, some hunter-gatherer groups show distinct cultural and biological traits in comparison to the early-Holocene ones. Such groups probably represent new populations inhabiting the SB, whose origin can be traced to the Middle Magdalena Valley, although other areas possibly played an important role. For instance, Correal (1990) found at Aguazuque (5025  $\pm$  40  $^{14}\text{C}$  BP), a broad-spectrum forager group, a distinct settlement pattern; remarkable differences in their mortuary practices (higher ritual complexity,

collective burials, position of the body and foreign grave goods), and atypical kinds of lithic tools, some of these made from foreign raw materials from the Middle Magdalena. In the Chía III site (5040  $\pm$  100  $^{14}\text{C}$  BP), some important differences were also detected (Ardila, 1984). Quoting Ardila (1984:43), “the lithic repertoire found in Chía III represents new series of artifacts neither described nor mentioned in any archaeological site in the region”. The mortuary behavior and the two excavated human skeletons also appear to be very different. In comparison to other mid-Holocene samples the Chía III crania (see also the Galindo I crania) have a very distinctive craniofacial morphology with wide and high faces, wide noses and maxilla and high and long neurocrania. On the other hand, the presence of extensive occlusal caries in these two individuals indicates a very different cariogenic diet (Ardila, 1984). In addition during the Aguazuque sequence between 5025  $\pm$  40 and 2725  $\pm$  35  $^{14}\text{C}$  BP, at Chía III (5040  $\pm$  100  $^{14}\text{C}$  BP) and at Galindo I (occupation level III: 7730  $\pm$  60–5000  $^{14}\text{C}$  BP), high amounts of lithic raw material and fauna (*Anodontile* and *Kinosternun postinginale*) from the Magdalena river Valley were found. Similar findings in Tequedama, El Abra, Tibitó, and Checua strongly suggest an ancient (as early as 11,000–10,000  $^{14}\text{C}$  BP) and well established contact network with the Magdalena Valley that effectively increased the rates of gene flow (Correal and van der Hammen, 1977; Gnecco, 2000). Another argument supporting the probable close relationship between the SB and the Magdalena Valley human populations is the relatively different diet of some mid-Holocene samples, as indicated by the isotopic signal of relatively high quantities of lowland tropical animal and vegetal resources (Cárdenas, 2002). In the local archaeological record, there are no diagnostic artifacts from the Middle Magdalena Valley such as projectile points, although other artifacts (i.e., scrapers) likely related to the Magdalena Valley have been found in some mid-Holocene sites from the SB region (Aguazuque, Chía III, Potreroalto and Galindo I).

The main arguments for the LEM are the persistence of the Abriense tradition over time, the gradual transformation of the subsistence systems, and the stability of craniofacial morphology. However the finding of distinct lithic tools morphofunctionally unrelated to the Abriense industry contradicts the “ubiquitous nature” of this technology and therefore its continuity. Likewise, the sole presence of the Abriense artifacts should not be interpreted as an indicator of population continuity, as it has been shown that this lithic kind is not necessarily a population marker but a very simple, versatile and multifunctional technology (Nieuwenhuis, 2002), which is reflecting environmental constraints and possibilities rather than persisting and culturally inherited patterns of behavior. In addition, the isotopic data disagree with the gradual economic transition inferred and suggest higher importance of vegetation resources during the early and mid-Holocene (Cárdenas, 2002). The  $\delta^{13}\text{C}_{\text{col}}$  values indicated that despite the presence of relatively distinct dietary patterns throughout the Holocene, is around 2000  $^{14}\text{C}$  BP when a significant change in the diet occurred. This means that, if there is a relationship between changes in the subsistence economy and morphological diversification, the differences observed in craniofacial morphology before that date likely are related to the entry of new morphologies to the region. Contrary to the analysis performed by Rodríguez (2007) and Neves et al. (2007), the present study, using additional statistical methods, a better control of the chronological framework of the samples analyzed and a higher number of early mid-Holocene crania, detected significant morphological changes throughout the Holocene. The results of discriminant and R-matrix analyses indicate high biological diversity which is incompatible to the existence of just one lineage morphologically stable for nearly 8000  $^{14}\text{C}$  years. Nevertheless, of



special interest are the results of the matrix correlation analysis which indicates that the morphological variation in the SB is congruent with a model of isolation by temporal distance and with just one scenario (PDM) suggestive of morphological discontinuity through time.

Additional supporting evidence on the population discontinuity comes from a site named Potreroalto located near Aguazuque (2 km) (Orrantia, 1997), in which two burials, lithic artifacts and archaeological fauna were found. The first burial contains a male skeleton dated by AMS to  $5910 \pm 70$   $^{14}\text{C}$  BP whose craniofacial morphology is almost identical to the Aguazuque foragers. This burial has high mortuary complexity (several good graves, lithic artifacts and the presence of ochre in the skeleton), although, differing from Aguazuque, the lithic artifacts are not Abriense, and the zooarchaeological record shows that rodents and rabbit (*Cavia aperea* and *Sylvilagus brasiliensis*) and not deer were the main meat source. This finding suggests that the Aguazuque-like hunter-gatherers arrived at least ca. 1000  $^{14}\text{C}$  years before and that their lithic repertoire and dietary preferences were different to most mid-Holocene SB foragers. The second burial contains a female skeleton dated by AMS in  $6830 \pm 110$   $^{14}\text{C}$  BP. Her craniofacial morphology is completely different to the male individual, and in contrast to the last burial, the mortuary record appears to be simpler, with a few lithic artifacts distinct to the Abriense kind. This evidence suggests two extra arguments in favor to the alleged mid-Holocene population change. First, if the Potreroalto individuals belong to the same set of subpopulations genetically-related to Aguazuque, it is clear that the Abriense lithic tradition was not always part of the lithic repertoire of the mid-Holocene foragers. This suggests that some foreign populations likely assimilated some cultural traits from the local ones and/or that such technology just reflects the availability of local raw material and environmental constrains (Nieuwenhuis, 2002). Second, if the distinctive morphology of the Potreroalto female (see also Chía III and Galindo I crania for different morphologies) disappeared during the mid-Holocene, this fact probably demonstrates that the lineage extinctions were relatively common in the past promoting population expansions and dispersal. Here, it is interesting to note that the paleoenvironmental record reveals that during the last 13,000  $^{14}\text{C}$  years the SB region was not a homogeneous landscape, indicating that different phenomena as ecological and climatic shifts produced important modifications (habitat fragmentation, reduction of species) (van der Hammen and González, 1960; van der Hammen and Correal, 1992). Such landscape changes from a biogeographic approach suggest repeated contraction–extinction and/or dispersal–expansion processes during the Holocene. This approach also suggests that the inferred landscape changes produced an uneven distribution of resources, which possibly required the cultural-hierarchization of the spaces used by humans (Borrero, 1989–1990). Accordingly, some microregions of the SB probably represented areas with special features (open and forest areas useful for deer hunting and/or the use of vegetation resources). If this model of cultural-hierarchical spaces is applied to the regional archaeological record, it becomes clear that the occupation of the SB should not be viewed as a linear and continuous process.

After the mid-Holocene, the local scenario changed significantly again. According to some authors, between 3000 and 2000  $^{14}\text{C}$  BP new population(s) (named Herrera) with different morphologies, pottery styles and with a subsistence system primarily based on agriculture arrived in the SB (Correal, 1990; Neves et al., 2007). Because very few human skeletal remains belonging to the Herrera period have been found, it is not possible to evaluate their morphological affinities with other samples. The craniofacial evidence shows that during the final-late Holocene (ca. 2000–1500

$^{14}\text{C}$  BP), new groups with distinct morphologies appeared at the SB. Such groups, named Muisca, according to the statistical analyses, have significantly distinct craniofacial patterns (i.e., broad faces and short neurocrania). The morphological differences found are not unexpected, because in the local archaeological literature the Muisca societies have important differences to all populations that inhabited the SB before them, including the presence of terracing agriculture, salt mine exploitation, high sociopolitical complexity, and broad commercial networks (Botiva, 1989; Langebaek, 1995). The biological affinities of the Muisca (data not shown) with the groups Panche – Lache from Boyacá and Northern Colombia and Guane from Santander and Norte de Santander provinces, suggest a common origin in the northeast region of Colombia. The Musica were one of the most important complex societies in the Colombian highlands and remained in the SB until the arrival of Spaniards in the 16th century.

## 5. Concluding remarks

The ideas above discussed suggest that the human history of the SB region was not a gradual process of *in situ* evolution, but on the contrary a more complex one affected by events of different nature, including climatic–environmental shifts, inter-societal contacts, contraction/extinction and population dispersal processes. The new ideas allow proposal of a scenario named Population Discontinuity Model (PDM) which states that in at least two moments, between 6000 and 3800  $^{14}\text{C}$  BP and between 2000 and 1500  $^{14}\text{C}$  BP, important population events, some of these likely influenced by climatic and ecological shifts, occurred. Those events include the extinction/dispersal of most SB population(s) and the arrival of new people from the Middle Magdalena Valley and surrounding areas during the mid-Holocene (ca. 6000–4000  $^{14}\text{C}$  BP), and the arrival of new agricultural Chibcha-speaking populations from the Magdalena Valley, central-east (Boyacá) and northeast Colombia (Santander and Norte de Santander) to the SB between ca. 2000–1500  $^{14}\text{C}$  BP. Although the chronological–environmental record and the morphological evidence suggest that appreciable population changes effectively occurred during mid-Holocene times, several important issues need to be clarified: 1) the events and processes that allowed that populations inhabiting the Magdalena river Valley expanded towards the SB; 2) the magnitude of the population changes (replacements, assimilations, etc) and 3) the role of the subsistence system changes in the population differentiation. The model of regional biocultural evolution outlined here represents an alternative to the traditional view about the human history of the SB that must be evaluated with more evidence.

## Acknowledgements

Special thanks to Gustavo Barrientos for his support and guidance along the way. I thank to F. Restifo and R. Huguin for inviting me to participate in this issue. Thanks to CONICET (Argentina) and FIAN (Colombia) for their financial support to this research. Several institutions and investigators gave me access to the skeletal collections under their care: Instituto de Ciencias Naturales and Laboratorio de Antropología Física, Universidad Nacional de Colombia (G. Peña and J.V. Rodríguez); Instituto Colombiano de Antropología e Historia (ICANH) (C.E. Piazzini); Museo Nacional de Colombia Bogotá (P. Ramirez and A. Bermúdez) and Departamento de Antropología, Universidad de Antioquia (A. Aceituno and N. Castillo). Thanks to Alexandra Delgado for the language corrections. Finally, thanks to the QJ editor, the guest editors and two anonymous reviewers for the useful comments provided during the reviewing process.

## References

- Aceituno, F.J., Loaiza, N., 2007. Domesticación del Bosque en el Cauca Medio Colombiano Entre el Pleistoceno Final y el Holoceno Medio. *British Archaeological Research International Series* 1654.
- Ardila, G., 1984. Chía un sitio precerámico en la Sabana de Bogotá. *Fundación de Investigaciones Arqueológicas Nacionales. Banco de la República, Bogotá*.
- Barrientos, G., Pérez, I., 2005. Was there a population replacement during the Late mid-Holocene in the southeastern Pampas of Argentina? *Archaeological evidence and paleoecological basis. Quaternary International* 132, 95–105.
- Borrero, L.A., 1989–1990. Evolución cultural divergente en la Patagonia Austral. *Anales del Instituto de la Patagonia (Serie Ciencias Sociales)* 19, 133–139.
- Botiva, C.A., 1989. La altiplanicie Cundiboyasence. In: Botiva, C.A., Cadavid, G., Herrera, L., Groot, A.M., Mora, S. (Eds.), *Colombia Prehispánica. Regiones Arqueológicas*. Universidad Nacional, Bogotá.
- Correal, G., 1990. Aguazuque: Evidencias de cazadores, recolectores y plantadores en la altiplanicie de la cordillera Oriental. *Fundación de Investigaciones Arqueológicas -Nacionales. Banco de la República, Bogotá*.
- Correal, G., van der Hammen, T., 1977. *Investigaciones Arqueológicas en los Abrigos Roccosos del Tequendama. Banco Popular, Bogotá*.
- Cárdenas, F., 2002. Datos sobre la alimentación prehispánica en la Sabana de Bogotá, Colombia. *Informes Arqueológicos. Instituto Colombiano de Antropología e Historia, Bogotá*.
- Darroch, J.N., Mosimann, J.E., 1985. Canonical and principal components of shape. *Biometrika* 72, 241–252.
- Delgado Burbano, M., Aceituno, F.J., Barrientos, G., 14C data and the early colonization of Northwest south America: a critical assessment. In: Miotti, L., Fleckenheimer, N., Salemme, M., Goebel, T. (Eds.), *The peopling of the Americas: a hundred years since the Ameghino-Hrdlika debate (1910-2010)*. Center for the Study of the First Americans. Texas A&M University, in press.
- Dillehay, T.D., 2000. *The Settlement of the Americas. A New Prehistory*. Basic Books.
- Dueñas, H., 1980. Variaciones climáticas del pleistoceno superior y del holoceno en la Sabana de Bogotá (estudio palinológico de la formación sabana). *Antropológicas* 2, 31–38.
- Gnecco, C., 2000. *Ocupación Temprana de Bosques Tropicales de Montaña*. Editorial Universidad del Cauca.
- Gómez, A., Berrío, J., Hooghiemstra, H., Becerra, M., Marchant, R., 2007. A Holocene pollen record of vegetation change and impact from Pantano de Vargas, and Intra-Andean basin of Duitama, Colombia. *Review of Paleobotany and Palynology* 145, 143–157.
- van der Hammen, T., Correal, G., 1992. El hombre prehistórico en la Sabana de Bogotá: datos para una prehistoria ecológica. In: van der Hammen, T. (Ed.), *Historia, Ecología y Vegetación. Corporación Colombiana para la Amazonia, Araraucara (Bogotá)*, pp. 211–230.
- van der Hammen, T., González, E., 1960. Upper Pleistocene and Holocene climate and vegetation of the Sabana de Bogotá (Colombia, South America). *Laidse Geologische Mededelingen* 25, 261–315.
- van der Hammen, T., Hooghiemstra, H., 1995. The El Abra stadial, a Younger Dryas equivalent in Colombia. *Quaternary Sciences Reviews* 14, 841–851.
- van der Hammen, T., Correal, G., van Klinken, G., 1990. Isotopos estables y dieta del hombre prehistórico en la Sabana de Bogotá (un estudio inicial). *Boletín de Arqueología* 5, 3–10.
- Howells, W.W., 1973. *Cranial Variation in Man. A Study by Multivariate Analysis of Pattern of Difference Among Recent Human Populations*. Papers of the Peabody Museum. Harvard University Press, Cambridge, Massachusetts.
- Hughen, K.A., Overpeck, J.T., Lehman, S.J., Kashgarian, M., Southon, J.R., Petersson, L.C., 1998. A new 14C calibration data set for the last deglaciation based on marine varves. *Radiocarbon* 40, 483–494.
- Ijzereef, G., 1978. Faunal remains from the El Abra Rockshelters (Colombia). *Paleogeography, Paleoclimatology, Paleoecology* 25, 163–177.
- Lahr, M.M., Foley, R., 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology* 41, 137–176.
- Langebaek, C., 1995. *Regional Archaeology in the Musica Territory. A Study on the Fúquene and Susa Valleys*. University of Pittsburgh Latin American Archaeology Publications. 9.
- López, C., 2008. *Landscape Development and the Evidence for Early Human Occupation in the inter-Andean tropical lowlands of the Magdalena River*. Syllaba Press, Colombia.
- Marchant, R., Behling, H., Berrío, J., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, R., Schreve-Brinkman, E., van Geel, B., van der Hammen, T., van Reenen, G., Wille, M., 2002. Pollen-based biome reconstructions for Colombia at 3000, 6000, 9000, 12000, 15000 and 18000 <sup>14</sup>C yr ago: late Quaternary tropical vegetation dynamics. *Journal of Quaternary Science* 17, 113–129.
- Mayewski, P.A., Rohling, E., Stager, J.C., Karlén, W., Maasch, K.A., Meeker, L.D., Meyerson, E.A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig, E.J., 2004. Holocene climate variability. *Quaternary Research* 62, 243–255.
- McLean, D., 1991. A climate change mammalian population collapse mechanism. In: Kainlauri, E., Johansson, A., Kurki-Suonio, I., Geshwiler, M. (Eds.), *Energy and Environment*. ASHRAE, pp. 93–100.
- Neves, W., Hube, M., Correal, G., 2007. Human skeletal remains from Sabana de Bogotá, Colombia: a case of Paleoamerican morphology late survival in South America? *American Journal of Physical Anthropology* 130, 1080–1098.
- Nieuwenhuis, C.J., 2002. *Traces on Tropical Tools: a Functional Study of Chert Artifacts from Preceramic Sites in Colombia*. Faculty of Archaeology, University of Leiden.
- Orrantia, J.C., 1997. Potreroalto: informe preliminar sobre un sitio temprano en la Sabana de Bogotá. *Revista de Antropología y Arqueología. Universidad de los Andes Bogotá* 9, 181–184.
- Relethford, J.H., Blangero, J., 1990. Detection of differential gene flow from patterns of quantitative variation. *Human Biology* 62, 5–25.
- Rodríguez, J.V., 2007. La diversidad poblacional de Colombia en el tiempo y espacio: estudio craneométrico. *Revista de la Academia Colombiana de Ciencias* 31, 321–346.
- Schafer, J.L., 1999. NORM 2.03. [http://www.stat.psu.edu/\\_jls/missoftwa.html](http://www.stat.psu.edu/_jls/missoftwa.html).
- Stuiver, M., Reimer, P., Reimer, R.W., 2005. CALIB 6.0. <http://intcal.qub.ac.uk/calib/>.
- Surovell, T., Brantingham, J.P., 2007. A note on the use of temporal frequency distributions in the studies of prehistoric demography. *Journal of Archaeological Science* 34, 1868–1877.
- Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.N., Mikhalevko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-year tropical climate history from Bolivian ice-cores. *Science* 282, 1858–1864.
- Vélez, M., Hooghiemstra, H., Metcalfe, S., Willie, M., Berrío, J., 2006. Late Glacial and Holocene environmental and climatic changes from a limnological transects through Colombia, northern south America. *Paleogeography, Palaeoclimatology, Palaeoecology* 234, 81–96.
- Weninger, B., Jöris, O., 2004. Glacial radiocarbon calibration. The CalPal Program. In: Higham, T., Bronk Ramsey, R.C., Owen, C. (Eds.), *Radiocarbon and Archaeology. 4th Symposium*. Oxford, 2002, Oxford University School of Archaeology, Monograph 62, pp. 9–15.
- Weninger, B., Jöris, O., 2008. A <sup>14</sup>C-age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in Western Eurasia. *Journal of Human Evolution* 55, 772–781.
- Williams, A., 2011. The use of summed radiocarbon probability distributions in archaeology: a review of methods. *Journal of Archaeological Science*. doi:10.1016/j.jas.2011.07.014.