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Holocene population history of the Sabana de Bogotá region, Northern South America: An assessment of the craniofacial shape variation

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Abstract

Objectives: Several authors using multiple and independent lines of evidence investigating the biocultural continuity versus discontinuity in the Sabana de Bogotá region, in the eastern highlands of Colombia, have arrived at contradictory conclusions supporting either scenarios. This study analyzes the craniofacial size and shape variation of diachronic samples from the study region to test distinct population history scenarios that support continuity or, alternatively, divergence.

Materials and methods: A total of 92 adult skulls belonging to five chronological groups, ranging from c. 10,100 to 350 ^{14}C YBP, were analyzed through Procrustean geometric morphometric techniques. Matrix correlation analysis, multivariate exploratory (PCA, FDA), and evolutionary quantitative genetic methods (R-matrix analysis and β-test) were used to study the diachronic craniofacial shape variation.

Results: A model that supports strong evolutionary diversification over the Holocene better explains the patterns of morphological variation observed. At least two periods of significant craniofacial size and shape change were detected: one during the middle to initial late Holocene transition (c. 4,000–3,200 ^{14}C YBP) and other toward the final late Holocene (post-2,000 ^{14}C YBP), which exhibit differences in the pattern and magnitude of cranial divergence. In addition, the differentiation viewed between early and mid-Holocene foragers could mark the initial entry of non-local populations into the region toward the beginnings of the middle Holocene.

Discussion: Distinct to previous investigations the present study supports a more complex regional population history where multiple population contractions/extinctions, dispersals and assimilations along with dietary adaptations took place during the last 10,000 years. These results are in agreement with the archaeological and paleoecological record which suggests marked periods of change rather than temporal stability.

KEYWORDS

biocultural discontinuity, Bogotá highplain, geometric morphometrics, Holocene, skull morphology

1 | INTRODUCTION

The Sabana de Bogotá (SB) in the eastern highlands of Colombia is a well-known archaeological region that has played an important role in the discussion of the initial human expansion into South America (Aceituno, Loaiza, Delgado, & Barrientos, 2013; Ardila, 1991; Correal, 1986; Delgado, Aceituno, & Barrientos, 2015b; Delgado, Aceituno, & Loaiza, 2015a; Dillehay, 2000). During the past 40 years, archaeological inves-

tigations have recovered abundant evidence including lithic tools, paleobotanical and zooarchaeological remains along with nearly one hundred burials with well-preserved human skeletal remains ranging from c. 10,100 to 4,000/3,500 ^{14}C YBP (Ardila, 1984; Correal, 1979, 1990; Correal & van der Hammen, 1977; Groot, 1992; Hurt, van der Hammen, & Correal, 1977; Orrantia, 1997). The post mid-Holocene archaeological record is even more profuse with large amounts of materials and hundreds of human skeletal remains (Botiva, 1988;

Correal, 1987; Enciso, 1990-1991). In addition, on the basis of palynological, glaciomorphological, diatom and isotopic evidence, detailed reconstructions of the predominant environmental conditions during the last 15,000 ^{14}C years have been performed (Boom, Mora, Cleef, & Hooghiemstra, 2001; Gómez, Berrío, Hooghiemstra, Becerra, & Marchant, 2007; Marchant et al., 2002; Mora & Pratt, 2002; van der Hammen, 1974; van der Hammen & Hooghiemstra, 1995; Vélez, Hooghiemstra, Metcalfe, Willie, & Berrío, 2006). Accordingly, the most accepted scenarios on the evolution of humans that inhabited the region since the late Pleistocene have been advanced on the basis of the study of lithic technology, raw material use and subsistence patterns, within a paleoenvironmental framework. Unfortunately, skeletal morphometric evidence has not been yet completely incorporated into the discussion, probably because previous studies solely described the patterns of morphological variation and did not integrated the archaeological and paleoenvironmental record in their explanation of the observed biocultural change.

2 | BIOCULTURAL CONTINUITY AND DISCONTINUITY SCENARIOS

The population history of the SB has been interpreted both as a process of *in situ* evolution (i.e., the continuous transmission of biological and cultural traits over a defined unit of time) and as a process of biocultural discontinuity (i.e., the cessation of transmission of those traits and eventually their replacement/assimilation by others; see below for a discussion of these concepts). Some authors have suggested since the late 1970s that specialized hunter-gatherers using the Abriense lithic industry penetrated the region during the late Pleistocene (*c.* 13,000 ^{14}C YBP) and remained there without major population, technological and economical shifts (except the entry *c.* 11,000 ^{14}C YBP and early disappearance *c.* 10,000 ^{14}C YBP of the Tequendamiense industry), until the arrival of agriculturalists during the initial late Holocene (*c.* 3,000 ^{14}CYBP) (Correal, 1990; Correal and van der Hammen, 1977; Hurt et al., 1977; van der Hammen, Correal, & van Klinken, 1990) or even until the arrival of European conquerors during the 16th century (Rodríguez, 2001). Based on the analysis of craniometric and odontometric traits, Rodríguez and colleagues (Rodríguez, 2001, 2007; Rodríguez & Vargas, 2010) indicated that the morphological patterns representing the same lineage undergo a progressive and subtle transformation throughout the Holocene. In their view, neither the arrival of foreign populations(s) nor changes in the subsistence system or environmental conditions promoted large craniofacial transformations/adaptations.

On the basis of distinct and independent lines of evidence, some authors gave support to the biocultural discontinuity scenario. During the late Pleistocene and early Holocene (*c.* 13,000–7,000 ^{14}C YBP), Dillehay (2000) detected important cultural changes including technological simplification and economic diversification apparently attributable to the entry of distinct groups. Nieuwenhuis (2002), identified a series of significant shifts in the lithic technology incompatible with the alleged existence of just one specialized and not very diverse lithic tradition among them: (i) the appearance of more complex artifacts;

(ii) the employment of foreign raw materials; (iii) the use of tools in non-specialized contexts and activities (i.e., broad spectrum economies) and (iv) the increasing importance of wood working and vegetable resources. Additionally, some authors suggested that the existence of intersocietal interactions and widespread exchange networks between the SB and other regions may have promoted biological and/or cultural population changes (Aceituno & Loaiza, 2007; Correal & van der Hammen, 1977; López, 2008; Nieuwenhuis, 2002). Cárdenas (2002) and Delgado (2016), using biochemical evidences (stable isotopes and trace elements), criticized the alleged economic specialization during the early Holocene, stressed the presence of early and mid-Holocene individuals with mixed C_3/C_4 diets that may indicate the entry of foreign lowland groups and suggested that the emergence of tropical crop horticulture during the initial late Holocene (*c.* 3,500 YBP) is related to population dispersals rather than an *in situ* development. Finally, some authors addressing the phenotypic diversity at the regional level suggested two distinct discontinuity scenarios. The first indicates that early hunter-gatherers with the "paleoamerican" morphology entered and evolved locally without strong phenotypic transformations until the initial late Holocene (*c.* 3,000 ^{14}C YBP) when they were completely replaced by foreign agricultural populations with an Amerindian cranial pattern (Neves, Hubbe, & Correal, 2007). The second suggests that remarkable changes in the craniodental and postcranial morphology occurred during the middle (*c.* 5,000–4,000 ^{14}C YBP) and late Holocene (*c.* post-2,500 ^{14}C YBP), probably associated with population retractions/extinctions and extensive contact as well as adaptations to environmental and subsistence shifts (Ardila, 1984; Cárdenas, 2002; Correal, 1990; Delgado, 2012, 2015, 2016; Gómez, 2012; Rodríguez Flórez & Colantonio, 2015).

3 | AIM AND HYPOTHESIS

As shown above, the various studies addressing the Holocene population history in the SB region have often arrived at contradictory results and the biocultural continuity/discontinuity dichotomy remains controversial. Therefore, the aims of the present investigation were as follows: (1) to analyze the phenotypic relationships among temporal groups from the SB region and (2) to evaluate the degree of biocultural continuity or discontinuity throughout the Holocene. Craniofacial morphogeometric data were used to evaluate a series of hypotheses (summarized below) that describe distinct population history scenarios related to the biocultural continuity/discontinuity based on archaeological, bioarchaeological and paleoecological evidence.

> *Hypothesis 1*. Human populations that inhabited the study region from the late Pleistocene until pre-conquest times presented very low biological diversity, minor morphological differences mostly related to changes in demography and shared the same pattern of variation. This hypothesis is based on craniometric and odontometric studies (Rodríguez, 2001, 2007; Rodríguez & Vargas, 2010). Under this hypothesis, samples belonging to different periods are

expected to show close biological similarities because they represent the same evolving lineage and are supposed to experience minor evolutionary diversification promoted by economic and/or environmental factors. In addition, given the existence of little cumulative biological modifications, slight differences between the extremes of the temporal range are expected.

Hypothesis 2. The pattern of craniofacial diversification is compatible with a model of isolation by temporal distance. According to this hypothesis, gradual change over time is expected due to the action of local microevolutionary processes. This implies that both biological and temporal distances will increase linearly whether a balance between gene drift and gene flow exists, with the first increasing and the second decreasing phenotypic divergence among samples (Delgado, 2012; Konigsberg, 1990).

Hypothesis 3. The SB populations evolved *in situ* with few biocultural changes until the initial late Holocene (*c*. 3,500–3,000 ^{14}C YBP) when extraregional agricultural populations arrived and replaced the local forager populations. This hypothesis is based on archaeological and craniometric studies (Correal, 1986; Correal & van der Hammen, 1977; Neves et al., 2007; van der Hammen et al., 1990). Under this hypothesis, populations from the early and middle Holocene or from the initial and final late Holocene should present strong phenotypic similarities. Additionally, distinct cranial patterns are expected for those samples inhabiting the region before and after the replacement event.

Hypothesis 4. Human populations inhabiting the SB region over the Holocene presented moderate biological variation and remarkable evolutionary diversification related to processes of contraction/extinction, population dispersals and adaptation. According to this hypothesis, environmental instability and population contacts promoted biological differentiation during the early, middle, and initial late Holocene. On the other hand, dietary adaptations, that is, size and shape changes occurring in different cranial regions but focused on the face and specifically on the masticatory complex affected the final late Holocene populations that experienced a strong change in subsistence strategies. This hypothesis is based on several archaeological, paleoecological, bioarchaeological and biochemical studies (Ardila, 1984; Cárdenas, 2002; Correal, 1990; Delgado, 2012, 2015, 2016; Marchant et al., 2002). Under this hypothesis, human populations exhibited a complex population history with periods of relatively strong biocultural change with a differential role of random and nonrandom factors in the morphological diversification. Therefore, it is expected that samples representing distinct temporal blocks present biological differences rather than similarities.

4 | MATERIALS AND METHODS

4.1 | The samples investigated

For the present study, several skeletal series (Figure 1; Table 1) representing distinct hunter-gatherer, horticultural and agricultural groups

were analyzed. Only adult individuals of both sexes with complete and well preserved crania were included which allows a relatively low sample size ($n = 92$), but span throughout the entire Holocene. Sex estimation was performed using standard diagnostic cranial and, when available, postcranial traits following White and Folkens (2005). Traditionally, local archaeologists divided the SB prehistory into three main periods of cultural/economic change, namely preceramic (hunter-gatherers *c*. 13,000–3,500 ^{14}C YBP); Herrera (early agriculture *c*. 3,000–1,200 ^{14}C YBP) and Muisca (late agriculture *c*. 1,150–350 ^{14}C YBP). However, because there is evidence that suggests important cultural, economic and biological differences between early and mid-Holocene hunter-gatherers (Ardila, 1984; Correal, 1990; Delgado, 2012), in the present study the preceramic period was divided in two periods. In addition, according to some authors (Langebaek, 1995) the Muisca period must be divided into early and late because there were noticeable differences in the level of agriculture intensification, population size, social organization and political complexity. Consequently, five chronological periods were formed including early-middle Holocene (EMH) *c*. 10,100–6,000 ^{14}C YBP ($n = 18$) and middle-Holocene (MH) *c*. 5,000–3,800 ^{14}C YBP ($n = 28$) hunter-gatherers; initial-late Holocene (ILH) *c*. 3,500–2,800 [14]CYBP ($n = 10$) horticulturalists and final-late Holocene intensive agriculturalists from the early Muisca (FLHEM *c*. 1,100–700 [14]CYBP; $n = 18$) and late Muisca (FLHLM *c*. 700–350 [14]CYBP; $n = 18$) periods. A detailed description of the samples that integrate the temporal blocks is presented in the Supporting Information in Appendix 1 (see also Neves et al., 2007 Appendix B).

4.2 | Procrustean geometric morphometric techniques

Two-dimensional procrustean geometric morphometrics techniques were used to investigate the diachronic morphological change. The skulls were photographed with a digital Samsung® S1070 camera (4.0 mega pixels of definition) following the standardized techniques recommended by Zelditch, Swiderski, and Sheets (2012). All skulls were photographed in lateral and frontal views and previous to the image capture, each specimen was oriented according to the Frankfurt plane. For the lateral view, the photographs were taken at 430 mm from the pterion point and for the frontal view were taken at 400 mm from the nasion point. In each image, a graded scale of 5 cm, as well as a label with the sex assigned, collection number, and population assignation were included.

Two different landmark/semilandmark configurations were investigated: (1) facial and (2) cranial. Landmarks and semilandmarks were digitized and processed using Geomorph package (Adams, Collyer, & Sherratt, 2015). For the facial configuration, 12 landmarks and 23 semilandmarks were digitized (Figure 2a), whereas for the cranial configuration, 15 landmarks and 13 semilandmarks were digitized (Figure 2b). Semilandmarks were aligned along the contour of the face and the cranial vault, sliding them along so as to minimize the Procrustes distance between the target and the reference by means of perpendicular projection or minimum Procrustes distance criteria (Bookstein, 1997). Original configurations were superimposed using the Generalized Procrustes Analysis to remove the effects of translation, rotation, and
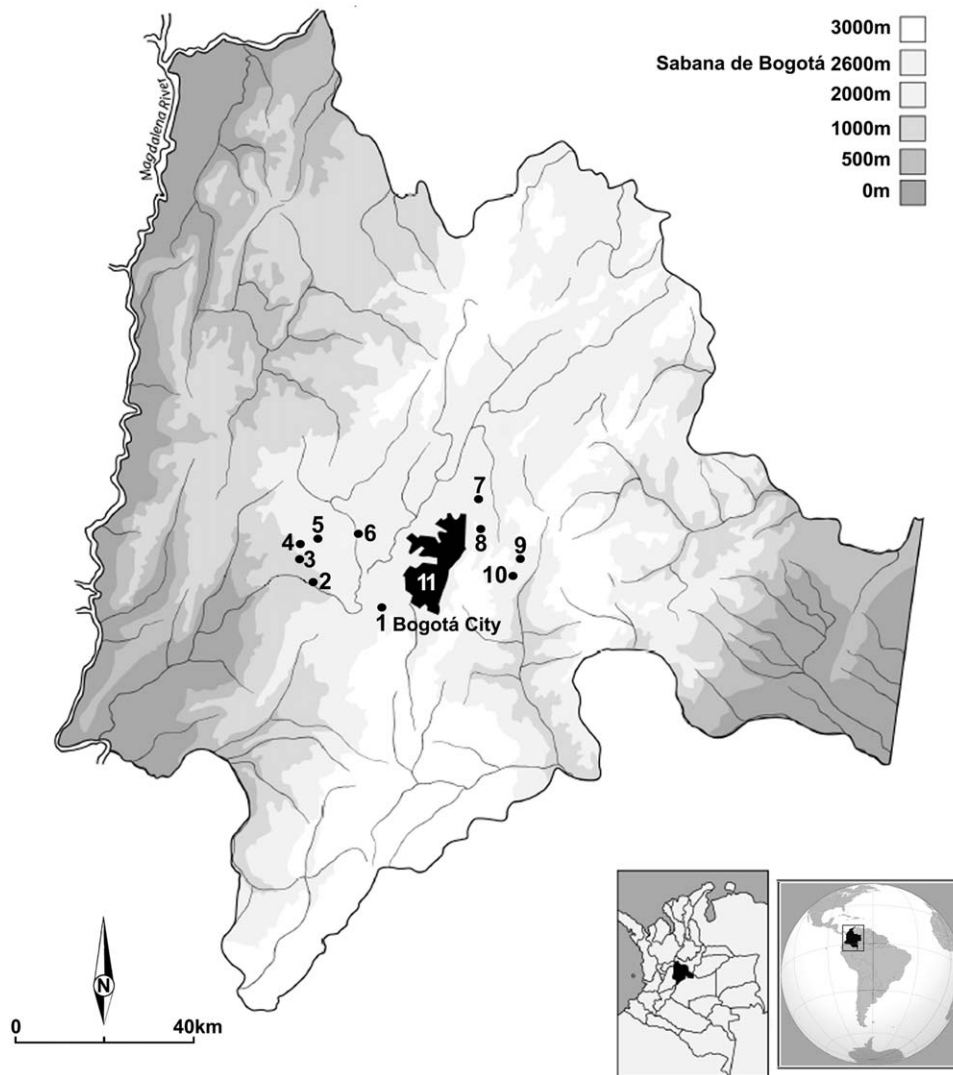
FIGURE 1 Map of the Sabana de Bogotá region showing the spatial distribution of archaeological sites with human skeletal remains investigated. The black area denotes the current geographical distribution of the City of Bogotá. 1 = Soacha; 2 = Tequendama; 3 = Aguazuque; 4 = Potreroalto; 5 = Vistahermosa; 6 = Galindo; 7 = Checua; 8 = Chía III; 9 = Sueva; 10 = Guavio; 11 = Muisca settlements from the City of Bogotá

TABLE 1 Composition of the samples analyzed in the present study

Sample	Site name	Main subsistence	Median ^{14}C dates (BP) and chronologic range	Sex	Number of individuals
Early/Middle Holocene (EMH)	Checua, Galindo, Guavio, Potreroalto, Sueva, Tequendama	Hunter- Gatherers	7235 *c.* 10,100–6000	10M/8F	18
Middle Holocene (MH)	Aguazuque, Chía III	Hunter- Gatherers	4527.5 *c.* 5000–3800	12M/16F	28
Initial late Holocene (ILH)	Aguazuque, Checua, Vistahermosa	Horticulturalists	3200 *c.* 3500–2800	8M/2F	10
Final late Holocene Early Muisca (FLHEM)	Las Delicias, Portalegre	Intensive agriculturalists	817.5 *c.* 1100–700	10M/8F	18
Final late Holocene Late Muisca (FLHLM)	Candelaria, Soacha	Intensive agriculturalists	575 *c.* 700–350	11M/7F	18
Total					92

Note. Laboratory codes for 14C dates are presented in the Supporting Information in Appendix 1.
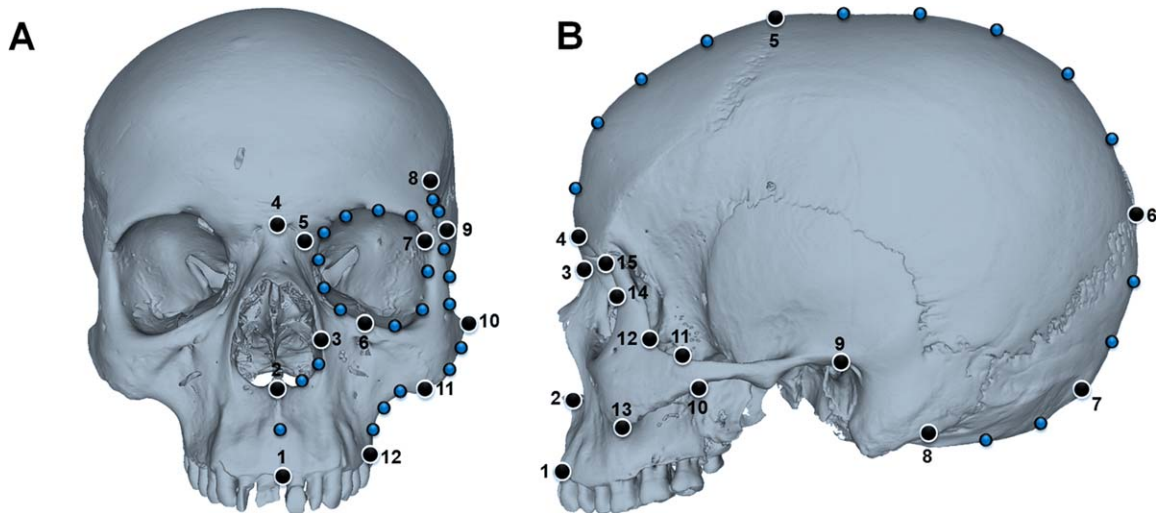
FIGURE 2 Landmarks (big circles) and semilandmarks (small circles) used in the analysis of two configurations facial (a) and cranial (b). (a) 1: prosthion; 2: nasoespinale; 3: alare; 4: nasion; 5: dacryon; 6: zygorbitale; 7: ectoconchion; 8: frontotemporale; 9; frontomalar temporale; 10: zygion; 11; zigomaxilare; 12: ectomolare. (b) 1: prosthion; 2: nasoespinale; 3: nasion; 4: glabella; 5: bregma; 6: lambda; 7: inion; 8: mastoidale posterior; 9: porion; 10: zygotemporale inferior; 11 zygotemporale superior; 12: jugale; 13: zygomaxilare; 14: orbitale posterior; 15: frontotemporale anterior

scaling (Zelditch et al., 2012). After superimposition, the shape was condensed in the aligned specimens, and skull size was expressed as the centroid size, the square root of the sum of squared distances of all landmarks of a skull from their center of gravity (Dryden & Mardia, 1998). After this procedure, the differences observed among landmark configurations were only due to shape. From the superimposed configuration, a mean shape of individuals was obtained (the consensus shape configuration) and used as a reference. The shape of each individual was defined by Procrustes residuals, which are the deviations of landmarks relative to the consensus (Zelditch al., 2012). As the Procrustes superimposition removes size but not the allometric component, a multivariate regression of the Procrustes coordinates on the centroid size was performed to obtain new shape variables (residuals). Several potential sources of error were evaluated to improve the dataset investigated (see Delgado, 2015). First, a standardized protocol was used to obtain images which ensure replicability. Second, only one investigator (the author) processed images and digitized landmarks and semilandmarks removing interobserver error. Third, after twice digitizing a subsample of skulls ($n = 10$), the intraobserver error was investigated through a repeated measures ANOVA to assess the average differences between both sections whose error was negligible (Delgado, 2015). Shape changes were represented both as TPS-grids and as wireframe diagrams. TPS-grids show deformations and color-coded Jacobian expansion/contraction factors which measure the degree of local expansion or contraction of the grid. Jacobian factors help with the visualization of shape changes because they highlight the region of the TPS-grid whose deformation corresponds to expansions or contractions according to a system of color coding. Scatterplots and ellipses of 95% confidence intervals were employed to visualize the data point distribution. Geomorph package v. 2.1.5 (Adams et al., 2015)

implemented in the free R software (R Core Team, 2015), MorphoJ (Klingenberg, 2011) and Past 3.06 (Hammer, Harper, & Ryan, 2001) programs were used to perform the statistical and graphical analyses.

4.3 | Testing hypothesis

Distinct hypotheses on the biological continuity and discontinuity were tested using design matrices and matrix correlation analysis. Thus, the correlation between the expected pattern of diversity under a specific hypothesis and the observed biological differentiation among samples, here expressed as unbiased D^2 distances (see below), was statistically evaluated through a two-way and three-way Mantel test (Mantel, 1967; Sokal, Oden, & Walker, 1997) using the Passage software (Rosenberg & Anderson, 2011). The critical α level was set at 0.05 and p values for Mantel tests were obtained after 9,999 permutations and corrected by the Bonferroni procedure for multiple comparisons. Model comparisons were performed using two D^2 matrices representing the two landmark configurations investigated. In the present study, four design matrices were constructed based on the previously formulated hypotheses (Table 2).

4.3.1 | Model 1 temporal continuity and minimal differentiation

This model represents the expected variation under Hypothesis 1, which suggests little morphological change in the SB region over the Holocene. According to this hypothesis, samples located at the extremes of the chronological range considered may present slight biological differences. Therefore, the distance between all samples was set to 0 excepting between EMH, FLHEM, and FLHLM, whose distance assigned was 0.5.

TABLE 2 Pairwise hypothesized distances according to five different models of population continuity and discontinuity for the SB region

Samples	Model 1	Model 2 (median ^{14}C dates)	Model 3	Model 4
EMH-MH	0	2707	0	0.5
EMH-ILH	0	4035	1	1
EMH-FLHEM	0.5	6418	1	1
EMH-FLHLM	0.5	6660	1	1
MH-ILH	0	1327	1	1
MH- FLHEM	0	3710	1	1
MH- FLHLM	0	3952	1	1
ILH- FLHEM	0	2383	0	1
ILH- FLHLM	0	2625	0	1
FLHEM- FLHLM	0	242	0	0

4.3.2 | Model 2 temporal structuring

Under this model, based on Hypothesis 2, biological distance among samples increases with time. Following Konigsberg (1990), the matrix of temporal distances was built considering the number of years between median radiocarbon dates for any pair of samples. Radiocarbon dates were obtained from archaeological reports (see Table 1 and Sup Mat 1) and grouped according to the temporal blocks used in this study.

4.3.3 | Model 3 initial late Holocene replacement

This model, based on Hypothesis 3, states that after ~8,000 years of *in situ* microevolution the craniofacial morphology of SB groups changed considerably *c.* 3,500/3,000 ^{14}C YBP due to a population replacement event. Accordingly, a distance of 0 was assigned if a pair of samples belongs to the same period before (EMH and MH) or after the replacement event (ILH, FLHEM, and FLHLM), whereas a distance of 1 was set when the comparison involved samples from different periods relative to the mentioned event.

4.3.4 | Model 4 strong evolutionary diversification

This model is derived from Hypothesis 4 and suggests remarkable biological differences among populations, representing distinct chronological periods. Under this hypothesis, maximum population differentiation is expected, therefore, all samples are separated by a distance of 1, except the pairs EMH-MH and FLHEM-FLHLM whose distances given were 0.75 and 0, respectively. The value of the first pair simulates the lesser biological diversification expected, relative to other periods, between early and middle Holocene populations and the value of the second pair stresses the biological similarity expected between both Muisca periods, despite their social/political, economic and demographic differences.

4.4 | Statistical tests

A Procrustes ANOVA was used to investigate the role of sexual dimorphism in the craniofacial size and shape variation within the entire sample. In addition, a *t*-test and box plots were used to assess the mean cranial size differences (logarithm of the centroid size) among the chronologic groups studied. Principal component analysis (PCA) and discriminant function analysis (DFA) were used to explore the between-group craniofacial shape differentiation. The DFA used here was implemented in MorphoJ and differs from the common DFA in that it evaluates the separation between just two groups of observations allowing the investigation of the differences between the mean shape of each pair of samples (Klingenberg, 2011). Mahalanobis (D^2) distances ($p < .01$) were calculated to assess the magnitude of the morphological dissimilarity between samples. Because the groups investigated have small sample sizes, D^2 distances were adjusted using the method proposed by van Vark and Bilsborough (1992) (see also Marcus, 1993) calculating an unbiased Mahalanobis distance Δ^2 as follows:

$$\Delta^2 = \frac{n-k-p-1}{n-k} \cdot D^2 - \frac{n_A+n_B}{n_A \cdot n_B} \cdot p$$

where n is the total sample size, k is the number of samples being compared, n_A and n_B are the sizes of the samples whose D^2 value is computed and p is the number of variables.

Other techniques from a model-bound approach were also used to assess the probable role of several evolutionary factors (e.g., gene drift, gene flow, and natural selection/phenotypic plasticity) shaping the craniofacial diversity. Such population genetic methods are based on several assumptions which may or may not be met in past human populations, nevertheless they provide a rough approximation to the regional population history and structure (see Marroig & Cheverud, 2004; Powell & Neves, 1999). The R-matrix method of intraregional differentiation by Relethford and Blangero (1990) was used to model the magnitude and direction of gene flow through time and the likely action of genetic drift. This model states that when populations within a region experience gene flow with an outside source at an equal rate, there will be a linear relationship between average within-group variation and genetic distance to the regional centroid. Populations will deviate from the model when they experience either greater than average or less than average extraregional gene flow relative to other populations in the region (Relethford & Blangero, 1990; Relethford, Crawford, & Blangero, 1997). Following von Cramon-Taubadel (2011), principal components (PC) were computed using the adjusted Procrustes coordinates (residuals) which were entered in the RMET 5.0 software (Relethford, 1997) as variables using a $h^2 = 1$ under the conservative assumption of complete heritability (for details see Relethford et al., 1997). As this model requires population sizes to be known and as there were probably differences in effective population sizes over the Holocene in study region, a weight coefficient of 1 was set to early and mid-Holocene hunter-gatherers and a value of 2 was set to late Holocene horticulturalists and agriculturalists. This implies that the last groups have a twofold population size. Despite the fact that prehistoric population size is difficult to be estimated and that there are no reliable estimates for the study region, the rough

TABLE 3 Results of Mantel and partial Mantel tests

Matrices	Correlation	Two-tailed p value	Two-tailed p value from permutation
Δ^2 (cranial) $\times$ Model 1	0.342	.258	.226
Δ^2 (cranial) $\times$ Model 2	0.565	.082	.083
Δ^2 (cranial) $\times$ Model 3	0.344	.373	.482
Δ^2 (cranial) $\times$ Model 4	0.889	***.014***	***.012***
Δ^2 (facial) $\times$ Model 1	0.100	.770	.756
Δ^2 (facial) $\times$ Model 2	0.115	.732	.704
Δ^2 (facial) $\times$ Model 3	0.164	.591	.491
Δ^2 (facial) $\times$ Model 4	0.648	**.037**	**.025**
Δ^2 (cranial) $\times$ Δ^2 (facial)	0.613	**.043**	**.039**
Δ^2 (cranial) $\times$ Model 1 (Model 2 constant)	−0.248	.446	.658
Δ^2 (cranial) $\times$ Model 3 (Model 2 constant)	0.005	.985	.990
Δ^2 (cranial) $\times$ Model 4 (Model 2 constant)	0.835	***.015***	***.014***
Δ^2 (facial) $\times$ Model 1 (Model 2 constant)	0.012	.969	.960
Δ^2 (facial) $\times$ Model 3 (Model 2 constant)	0.119	.693	.736
Δ^2 (facial) $\times$ Model 4 (Model 2 constant)	0.715	**.049**	**.041**

Note. **In bold** - models considered statistically significant ($p < .05$). ***In bold italics*** - models considered significant after the Bonferroni correction. P-values after 9,999 permutations.

values used are based on archaeological studies that suggest that late Holocene populations presented much larger site and cemetery sizes (and hence population size) than early and mid-Holocene populations (Correal, 1990; Correal & van der Hammen, 1977; Langebaek, 1995).

Additionally, the β-test of Ackermann and Cheverud (2004) based on the theoretical assumptions of Lande (1979, 1980) was used to evaluate whether the craniofacial diversification seen over the Holocene in the study region could be explained by genetic drift alone or whether nonrandom processes like selection and phenotypic plasticity played an important role. According to the genetic population theory, if the population divergence is related to stochastic evolutionary factors alone, there must be a proportional relationship between the levels of phenotypic variation within and between groups (Lande, 1979). Alternatively, if this relationship is not proportional, it is likely due to non-stochastic mechanisms. To test the proportionality of variances, the β-test uses a regression of among-group variances on within-group variances for the PC of shape variables. Population variance/covariance (V/CV) phenotypic matrix (**W**) was used as a proxy of the additive genetic V/CV matrix (**G**) as the proportionality between **W** and **G** (Cheverud, 1988; Martínez-Abadías et al., 2012) has been demonstrated for human craniofacial morphological traits. Following Ackermann and Cheverud (2004), the Lande's (1979) quantitative model for understanding the relationship between morphological change and variation/covariation under genetic drift was used, which is shown by the equation

$$B_t = G(t/N_e),$$

where B_t is the between-population V/CV matrix (dispersion matrix), in generation t, **G** is the additive genetic V/CV matrix of the founding pop-

ulation from which the group of populations is derived, and N_e is the effective population size (Lande, 1979, 1980; Lofsvold, 1988). Given the proportionality between the within-group phenotypic V/CV matrix (**W**) and the additive genetic V/CV matrix (**G**) for cranial morphological traits in humans (Martínez-Abadías et al., 2012), the substitution of **G** for **W** results as follows

$$B \propto W(t/N_e),$$

where N_e and t are constants for any particular comparison, and therefore the expected pattern of between-group phenotypic variation should be proportional to the within-group phenotypic variation (**B** $\propto$**W**), if the populations have diversified by random evolutionary processes. Similarly, if these patterns of variation are not proportional, other modes of evolutionary phenotypic divergence, such as differential selection, may have been at work. According to Ackermann and Cheverud (2004), the relation between W and B can be written as a linear

TABLE 4 Procrustes ANOVA for the sex factor (size and shape) for the two landmark configurations investigated

Configuration		Sums of squares	Mean squares	df	Goodals F	P value
Cranial	Size	0.0001	0.0001	1	1.83	.1806
	Shape	0.0050	0.0001	50	2.27	**.0001**
Facial	Size	0.0000	0.0000	1	0.14	.7094
	Shape	0.0065	0.0009	66	1.19	.1430

Note. **In bold** significant p-values.

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TABLE 5 Size (log SC) differences between chronological groups in the two landmark configurations investigated

Group	EMH	MH	ILH	FLHEM	FLHLM
EMH	0	0.271	0.749	−0.813	0.431
MH	−1.635	0	0.597	−1.292	−0.191
ILH	−0.774	**−2.413**	0	−1.861	0.502
FLHEM	0.005	−1.412	0.671	0	−1.565
FLHLM	0.060	−1. 350	0.724	−0.004	0

Note. Above of the diagonal *t*-values for the facial configuration and below of the diagonal *t*-values for the cranial configuration. **In bold** significant *t*-values ($p < .05$).

regression equation after a PCA. On a logarithmic scale, this equation can be written as

$$1nB_i = 1n(t/N_e) + \beta 1n(W_i),$$

where B_i is the between-population variance and W_i is the within population variance for the *i*th eigenvector extracted from W, t is time in generations and N_e is effective population size. If differentiation was produced by genetic drift, we expect a regression slope (β) of 1.0 for the regression of between- on within-population variance. A significant deviation from a slope of 1.0 indicates a pattern not likely to have been produced by genetic drift; no significant or no deviation from 1.0 means we have failed to reject the null hypothesis of drift, leaving other non-random evolutionary processes such as selection and phenotypic plasticity as an alternative. Regression slopes significantly >1.0 indicate that one or more of the first PCs are more variable, relative to other PCs, than expected under a model of drift, whereas slopes <1.0 indicate that populations are relatively highly divergent among minor PCs. Ackermann and Cheverud (2004), showed that under a strictly neutral evolutionary model, increasing divergence time will also increase the dispersion among groups and consequently the regression constant (t/N_e), but this does not alter the expectation of 1.0 for the regression slope. The beta test was performed in the free R software (R Core Team, 2015).
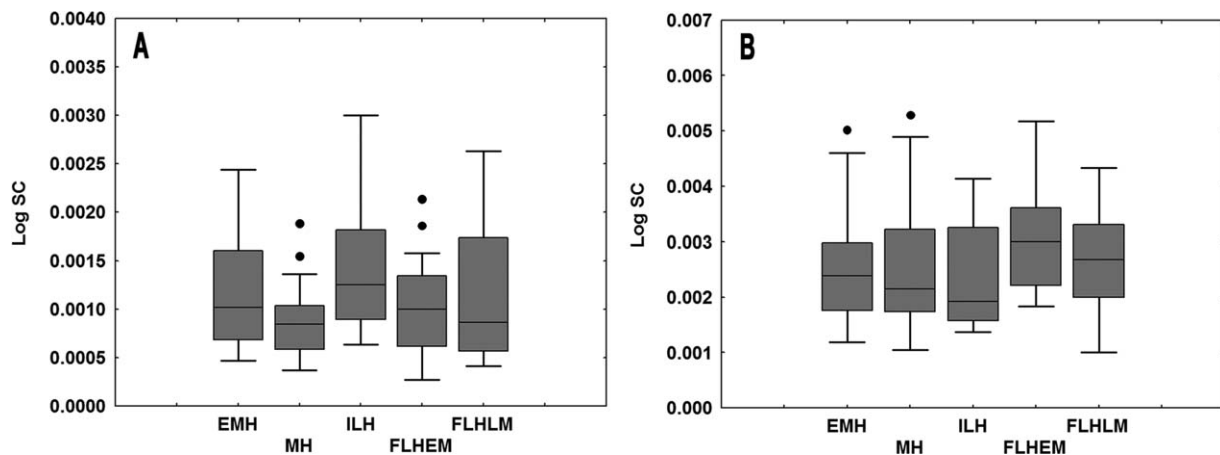
5 | RESULTS

5.1 | Matrix correlation analysis

The results of the Mantel and partial Mantel tests are presented in Table 3. Only the model that suggests strong evolutionary diversification presented significant correlations with cranial and facial shape distances, even after Bonferroni correction. When time was held constant, Models 1 and 3 presented very low correlations indicating that the alleged *in situ* microevolution is the less plausible scenario. As expected, facial and cranial distance matrices are significantly correlated, demonstrating that both configurations reveal similar evolutionary histories.

5.2 | Descriptive analysis

The Procrustes ANOVA results (Table 4) showed significant shape, but no size differences between males and females for the cranial configuration. The facial configuration presented neither shape nor size differences between sexes. The *t*-test revealed no major size differences among groups, except the comparison between MH hunter-gatherers and ILH horticulturalists for the cranial configuration (Table 5).The box plots corroborated the post-middle Holocene size fluctuation in the groups investigated (Figure 3).

5.3 | Exploratory analysis

5.3.1 | Principal component analysis

The results of the PCA investigating the craniofacial shape differences are presented in Figures 4 and 5. For the cranial configuration (Figure 4), there exist important shape differences between the groups investigated and the 95% ellipses show relatively well defined clusters through the morphospace. According to the shape changes, the EMH and MH hunter-gatherers, represented by high negative and low positive scores in the PC1 (29.3% of the total variance), have long and low vaults with projected faces, high and relatively retracted zygomatics
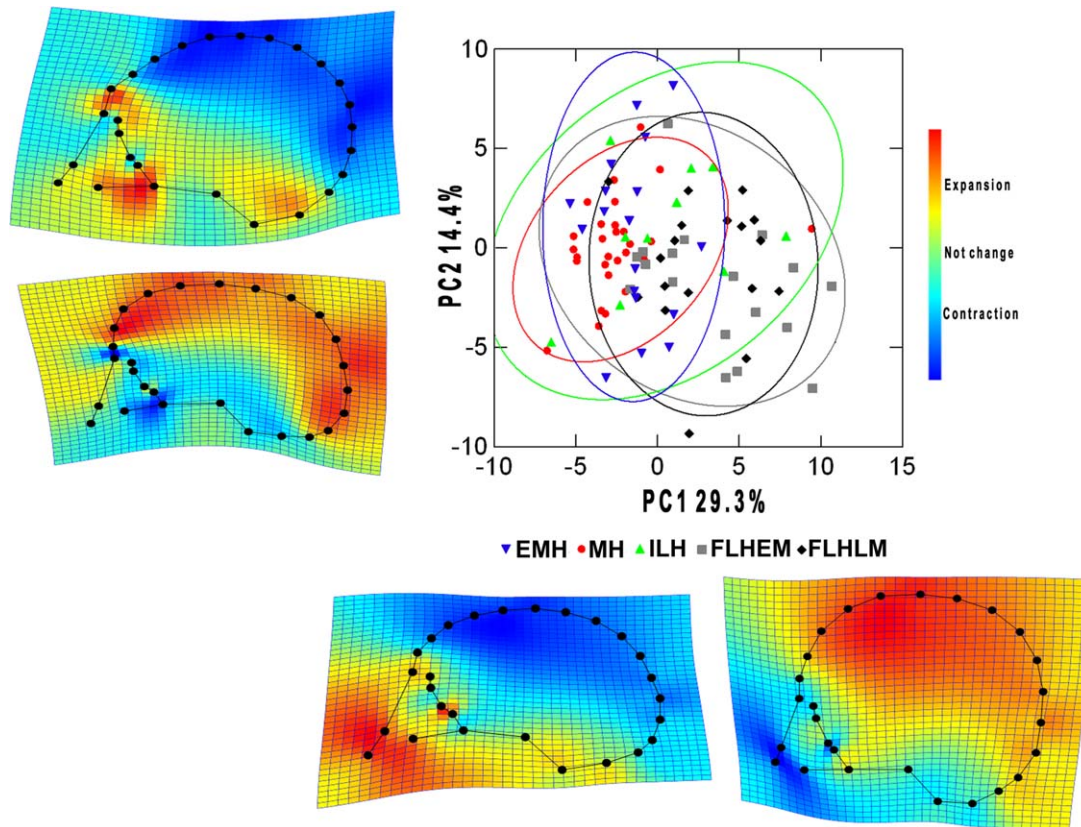

FIGURE 3 Boxplots showing the cranial (A) and facial (B) size variation (log CS) between the samples studied. EMH: early/middle Holocene; MH: middle Holocene; ILH: initial late Holocene; FLHEM: final late Holocene early Muisca; FLHLM: final late Holocene late Muisca

FIGURE 4 Scatterplot of the first two principal components (43.7% of the total variance) for the cranial configuration. Shape changes are represented as TPS-grids showing deformations for the PC positive/negative scores and colored coded Jacobian expansion/contraction factors which measure the degree of local expansion or contraction of the grid. Yellow to red factors indicate expansions and light to dark blue factors indicate contractions. The green color indicates areas with few or no changes. Scale factor of the grid 0.1 units. Ellipses of the 95% of confidence intervals are presented for the inverted triangles (early/middle Holocene hunter gatherers: EMH); circles (middle Holocene hunter-gatherers: MH); triangles (initial late Holocene horticulturalists: ILH); squares (final late Holocene early Muisca agriculturalists: FLHEM) and diamonds (final late Holocene late Muisca agriculturalists: FLHLM)

and high noses and orbits, while the FLH agriculturalists represented by the high positive and low negative scores presented short and high vaults with retracted faces, low zygomatics, nose and orbits. The ILH horticulturalists have a cranial pattern that suggests more rounded cranial vaults, relatively projected faces, low noses and high orbits. Jacobian factors (Figure 4) show a contracted cranial vault and expanded face/temporal bone in EMH hunter-gatherers and the opposite pattern among FLH agriculturalists. PC2 (14.4% of the total variance) presented more diffuse clusters without a clear inter-group differentiation, although it resembles the shape distinction viewed in PC1. Jacobian factors show a contraction/expansion pattern that highlights differences in the cranial vault, occipital bone, zygomatics, and glabella.

The PCA, investigating the facial module (Figure 5), reveals more among-sample dissimilarity than cranial configuration, while 95% ellipses show highly differentiated clusters. In PC1 (22.7% of the total variance), facial shape changes indicate that EMH and MH hunter-gatherers (high/mean positive and low negative scores) have narrow and high faces, small orbits, high and narrow noses and constrained zygomatics while FLH agriculturalists (negative scores) present broad and low faces and noses, large orbits and enlarged zygomatics. The ILH horticulturalists did not present a clearly defined facial shape, with no

clear differentiation from hunter-gatherers and agriculturalists. Jacobian factors for PC1 show expansion in maxilla, frontotemporal/frontomalar and mid-facial regions as well as contraction in the zygomatics among EMH and MH hunter-gatherers and the contrary pattern among FLH agriculturalists, that is, contraction in the middle face, frontomalar region and maxilla. PC2 (13% of the total variance) show that EMH/MH hunter-gatherers and ILH horticulturalists are mostly restricted to the negative scores, while FLH agriculturalists are widely distributed throughout PC2 (positive and negative scores). PC2 shape changes indicate intermediate forms to those visualized in PC1 with less marked differentiation. Jacobian factors along PC2 reveal that the facial regions with the highest variation correspond to the maxilla and zygomatics and to a lesser extent in the orbits and nose.

Although the EMH and MH groups in both PC analyses (Figures 4 and 5) appear similar to each other when compared with late Holocene samples, an independent PCA investigating both samples (Figures 6 and 7) shows marked shape differences with well defined clusters as indicated by the ellipses of 95% confidence intervals. Figure 6 (PC1 22.2% of the total variance) shows that while EMH foragers represented by positive scores have relatively short, rounded, and low vaults with retracted/short faces, MH foragers represented by negative
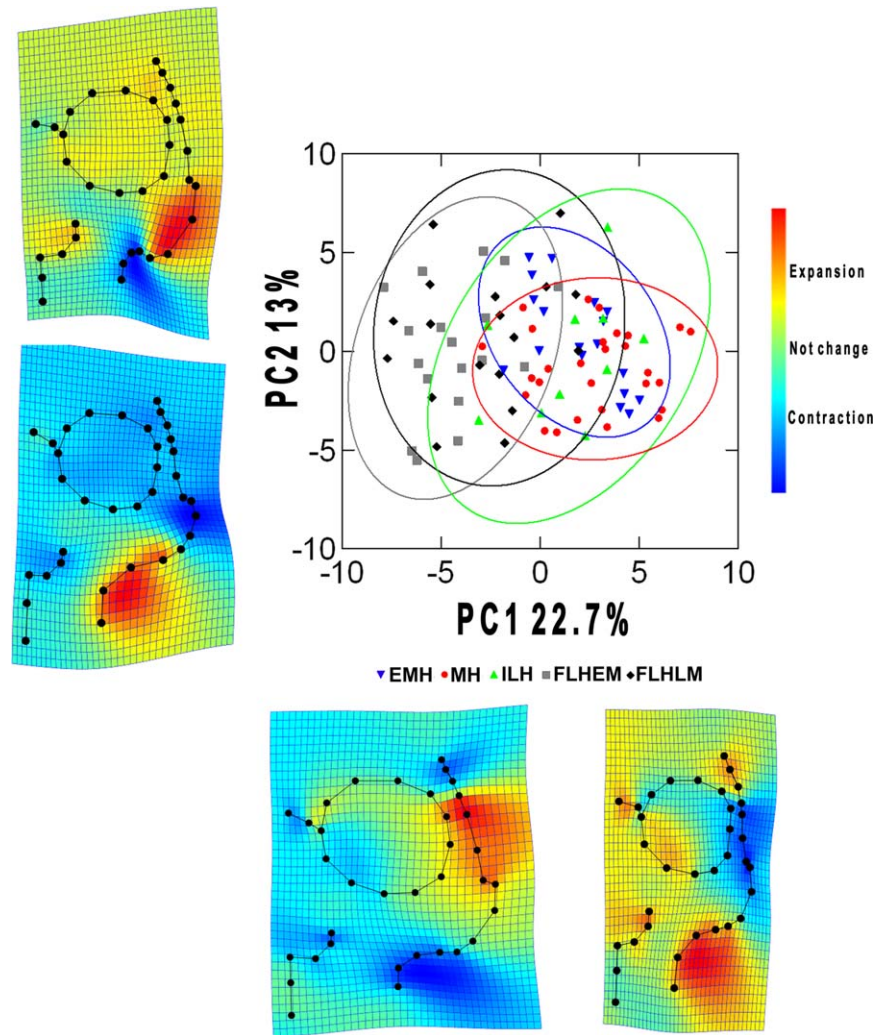
FIGURE 5 Scatterplot of the first two principal components (35.7% of the total variance) for the facial configuration. Shape changes are represented as TPS-grids showing deformations for the PC positive/negative scores and colored coded Jacobian expansion/contraction factors which measure the degree of local expansion or contraction of the grid. Yellow to red factors indicate expansions and light to dark blue factors indicate contractions. The green color indicates areas with few or no changes. Scale factor of the grid 0.1 units. Ellipses of the 95% of confidence intervals are presented for the inverted triangles (early/middle Holocene hunter-gatherers: EMH); circles (middle Holocene hunter-gatherers: MH); triangles (initial late Holocene horticulturalists: ILH); squares (final late Holocene early Muisca agriculturalists: FLHEM) and diamonds (final late Holocene late Muisca agriculturalists: FLHLM)

scores have the contrary pattern, that is, long, tall, and high vaults as well as projected faces and zygomatics. The pattern of shape expansion/contraction showed by the Jacobian factors along PC1 indicates frontal, temporal and parietals expanded in EMH and contracted in MH plus contracted faces and zygomatics among EMH and expanded in MH hunter-gatherers. In the PC2 (14.1% of the total variance), the Jacobian factors show changes in the occipital and temporal bones, the zygomatics and the face, although without a clear pattern of differentiation between both groups. Finally, Figure 7 (PC1 25.2% of the total variance) also shows a pattern of dichotomic facial shape differentiation between EMH and MH foragers. MH individuals (positive scores) have overall wide and high faces plus contracted maxilla, while EMH hunter-gatherers (negative scores) have expanded maxilla as well as narrow and low faces. PC2 (14.1% of the total variance) highlights differences in the low and mid-face between the extremes of the positive

and negative scores but a clear distinction is not evident because individuals representing EMH and MH foragers are indistinctly scattered throughout the PC2 shape space.

5.3.2 | Discriminant function analysis

The results of DFA are presented in Figures 8 and 9 and Table 6. The mean shapes for the cranial configuration appear in Figure 8. There are significant differences throughout the temporal vector. Although there is no progressive differentiation, there are important fluctuations. For instance, the MH hunter-gatherers presented differences with the late Holocene samples (i.e., ILH, FLHEM, FLHLM), even more than EMH hunter-gatherers. The shape changes are concentrated in the cranial vault and temporal bone, zygomatics and maxilla and, to a lesser extent, in the lower face. The two FLH agriculturalist samples are overall very similar to each other with mostly the same cranial configuration. ILH
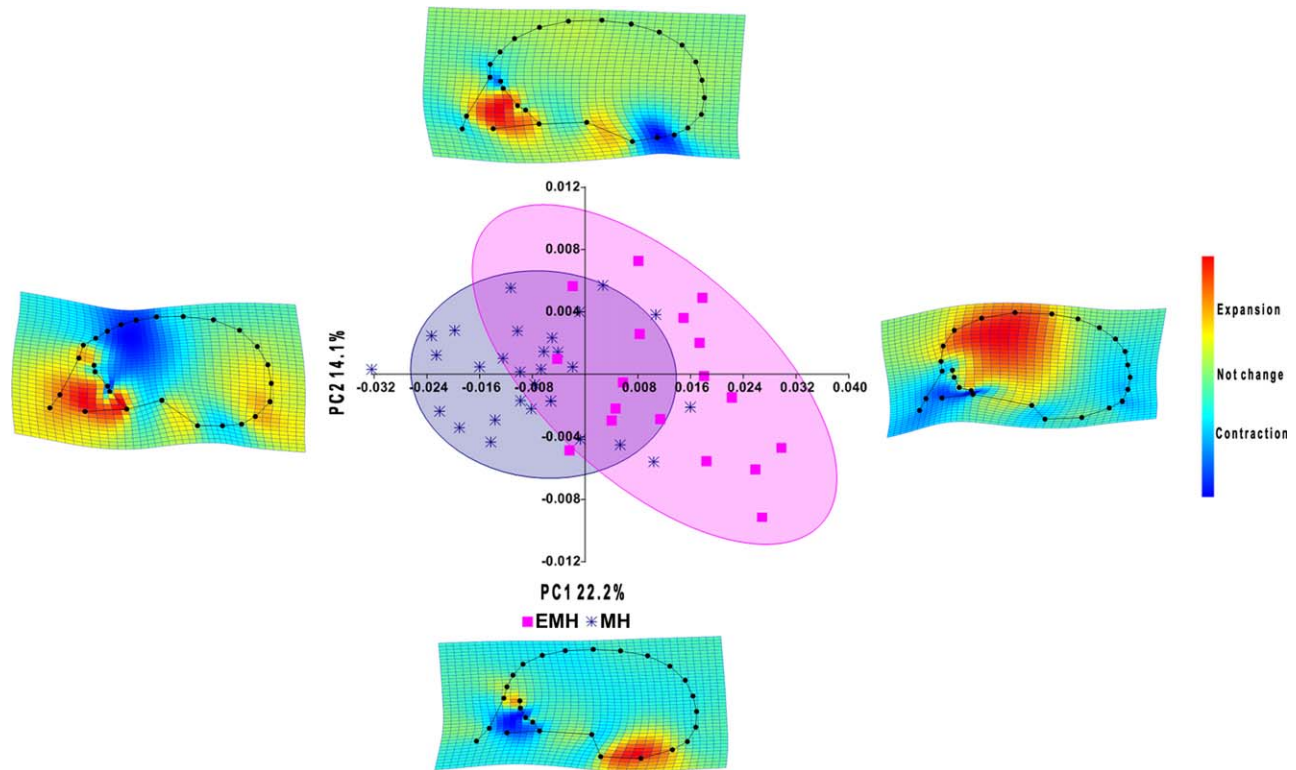
FIGURE 6 Scatterplot of the first two principal components (36.3% of the total variance) for the cranial configuration. Shape changes are represented as TPS-grids showing deformations for the PC positive/negative scores and colored coded Jacobian expansion/contraction factors which measure the degree of local expansion or contraction of the grid. Yellow to red factors indicate expansions and light to dark blue factors indicate contractions. The green color indicates areas with few or no changes. Scale factor of the grid 0.1 units. Ellipses of the 95% of confidence intervals are presented for squares (early/middle Holocene hunter-gatherers: EMH) and stars (middle Holocene hunter-gatherers: MH)

horticulturalists presented some differences with EMH and MH hunter-gatherers and are distinct from FLH agriculturalists. The main differentiation between ILH and MH samples lies on the lower face as well as on the frontal and temporal bone, while between ILH and FLH samples are focused on the cranial base, zygomatics and maxilla as well as the lower face. The main trends of shape changes in the facial module are depicted in Figure 9. All groups presented deep differences over time, even among continuous periods. For instance, EMH and HM differ in the maxilla and upper facial region, whereas MH and ILH in zygomatics and maxilla. ILH and FLHEM/FLHLM differ in several facial features. Overall specialized agriculturalists have wider orbits, zygomatics and maxilla and shorter noses than hunter-gatherers. Similar to the cranial configuration, there is morphological divergence over time and a remarkable temporal differentiation.

Table 6 shows corrected Δ^2 distances between pairs of groups according to the facial and cranial configuration. These results reinforce the PCA and stress the divergence that occurred after the middle Holocene. Except the comparison between EMH-MH and FLHEM-FLHLM, all significantly differ in statistical terms. Interestingly, biodistance analysis does not support a pattern of linear temporal dissimilarity, but shows fluctuations around the middle and initial late Holocene and an important cranial and facial diversification during the final late Holocene (last 2,000 years BP). The magnitude of differentiation is more

pronounced in the face than in the general cranial configuration, which makes sense given the higher plasticity of the face in modern humans likely related to its longer skeletal growth trajectory and multiple and complex functions (Lieberman, 2011; Moss & Young, 1960).

5.4 | Evolutionary quantitative genetic analysis

Results of the R-matrix analysis are presented in Tables 7 and 8 for the groups investigated using both landmark configurations. Table 7 presents the minimum F_{ST} values for different arrays of the total set of samples, which suggest relatively similar patterns of temporal differentiation in both configurations, although they exhibit different proportions of phenotypic variance. The average regional F_{ST} value for both modules suggests relatively low or moderate biological diversity. These values are greater than individual comparisons, indicating higher variation among than within regions. Interestingly, the regional F_{ST} values for the SB region are greater than those from other American regions which experienced extraregional gene flow (Steadman, 2001; Varela & Cocilovo, 2002). In temporal terms, EMH and MH hunter-gatherers have relatively low diversity as viewed from their F_{ST} values. When the initial late Holocene sample was considered, the F_{ST} increased noticeably almost reaching the regional value and the final late Holocene samples have the lowest diversity. In a similar way, the results of the
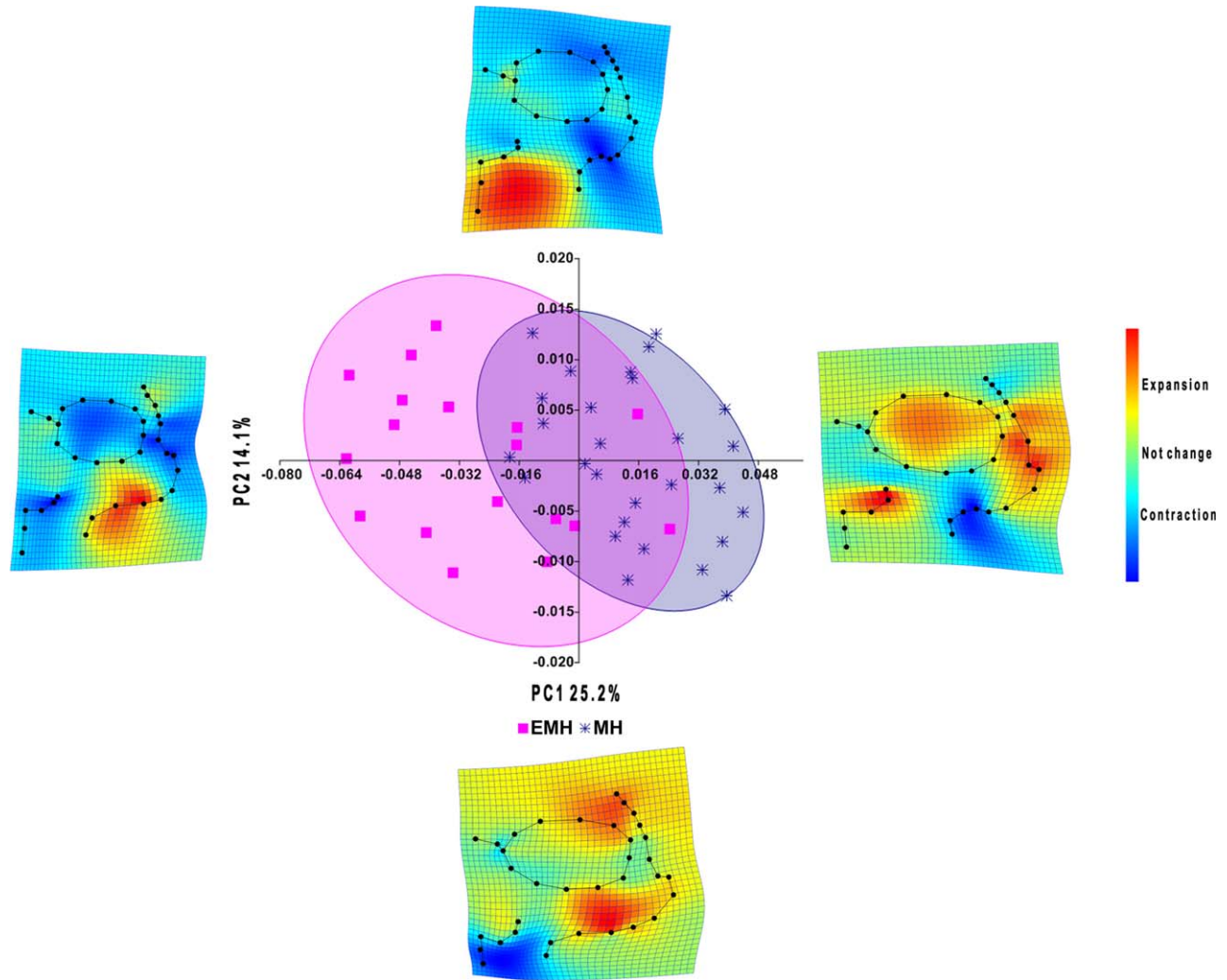
FIGURE 7 Scatterplot of the first two principal components (39.3% of the total variance) for the facial configuration. Shape changes are represented as TPS-grids showing deformations for the PC positive/negative scores and colored coded Jacobian expansion/contraction factors which measure the degree of local expansion or contraction of the grid. Yellow to red factors indicate expansions and light to dark blue factors indicate contractions. The green color indicates areas with few or no changes. Scale factor of the grid 0.1 units. Ellipses of the 95% of confidence intervals are presented for squares (early/middle Holocene hunter-gatherers: EMH) and stars (middle Holocene hunter-gatherers: MH)
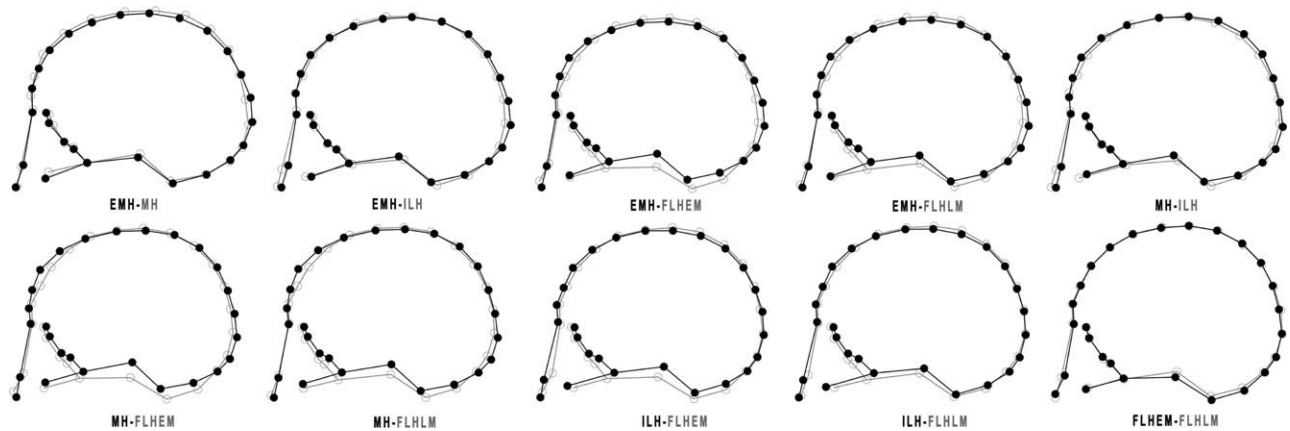

FIGURE 8 Wireframe visualization of cranial shape changes after a discriminant function analysis. Landmarks colors (black and gray) correspond to the mean shapes of each pair of samples compared (codes mentioned in Table 1). Scale factor of the wireframes 5.0 units
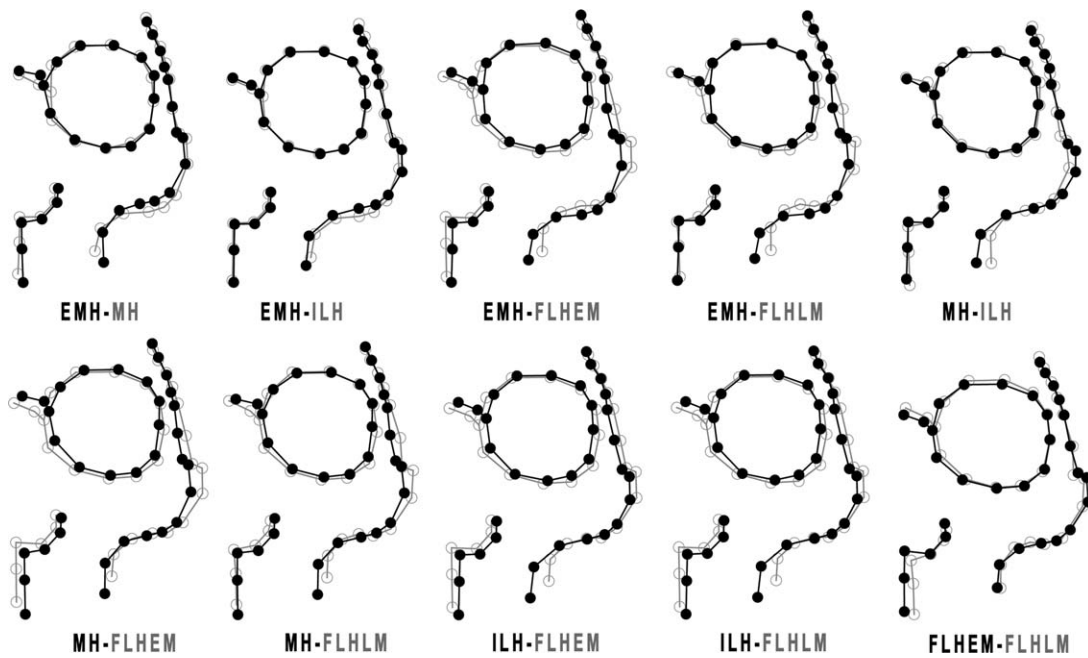
FIGURE 9 Wireframe visualization of facial shape changes after a discriminant function analysis. Landmarks colors (black and gray) correspond to the mean shapes of each pair of samples compared (codes mentioned in Table 1). Scale factor of the wireframes 5.0 units

within-group phenotypic variance analysis (Table 8) indicated that final late Holocene samples have loss of diversity (negative residual variance). The positive residual variance viewed in the ILH samples also agrees with its high F_{ST} value as it indicates more variation than expected. The early and middle Holocene samples presented greater than expected within-group phenotypic variation. The group farthest from the average of the total population in both configurations was MH (cranial r_{ii} 0.0639 and facial r_{ii} 0.0606), indicating high genetic divergence.

Finally, the regressions of logged between-group variation against logged within-group variation are presented in Table 9. The slope was significantly less than 1 in both configurations independent of whether the variables were corrected or not for allometry. This indicates, on the one hand, that size does not contribute to the rejection of the neutrality hypothesis and, on the other, that the first few eigenvectors may have relatively too little between-population variation compared with the smaller eigenvectors for divergence caused by drift alone. The R^2

values for both configurations using corrected and uncorrected variables indicated that a substantial proportion of variation was shared (c. 90–92%) between the within- and among-population variances. Another interesting result is the correspondence, regarding the rejection of the hypothesis of exclusive evolution by genetic drift, between distinct modules (facial and cranial), which suggests similar responses to directional evolutionary factors in both cranial configurations. These results reveal that there is a greater variation than expected if only random processes were involved in the phenotypic divergence observed, leaving other directional factors such as selection and phenotypic plasticity responsible for the disproportionality between among- and within-population craniofacial variation.

6 | DISCUSSION

6.1 | Temporal and economic trends on craniofacial shape divergence

Results revealed remarkable population differentiation through time. Such a population history scenario, according to the matrix correlation analysis, best fits the strong craniofacial diversification viewed. Two periods of significant craniofacial size and shape change were detected throughout the chronological range considered, one during the middle to initial late Holocene transition (c. 4,000–3,200 ^{14}C YBP) and the other toward the final late Holocene (post-2,000 ^{14}C YBP) which exhibit differences in the pattern and magnitude of the cranial shape variation. In addition, the distinction between early and middle Holocene foragers could mark the initial entry of foreign populations into the SB region toward the beginnings of the middle Holocene.

TABLE 6 Corrected Δ^2 distances between chronological groups from the SB region

Group	EMH	MH	ILH	FLHEM	FLHLM
EMH	0	**7.24**	**10.04**	**9.14**	**10.47**
MH	4.29	0	**10.55**	**9.60**	**8.55**
ILH	**5.54**	**5.80**	0	**11.16**	**10.64**
FLHEM	**7.23**	**5.66**	**7.04**	0	**8.27**
FLHLM	**6.05**	**6.36**	**6.78**	2.60	0

Note. Above of the diagonal distance values for the facial configuration and below of the diagonal distance values for the cranial configuration. **In bold** significant Δ^2 distances ($p < .01$).

TABLE 7 Minimum F_{ST} values for cranial and facial landmark configurations for the samples investigated

Landmark configuration	Samples and chronological range	Minimum F_{ST}	Standard error
Cranial	EMH, MH (10,100-3800 ^{14}C YBP)	0.0293	0.005
	ILH, FLHEM, FLHLM (3500-350 ^{14}C YBP)	0.0438	0.005
	FLHEM, FLHLM (1100-350 ^{14}C YBP)	0.0143	0.003
	Total	0.0522	0.004
Facial	EMH, MH (10,100-3800 ^{14}C YBP)	0.0010	0.004
	ILH, FLHEM, FLHLM (3500-350 ^{14}C YBP)	0.0316	0.006
	FLHEM, FLHLM (1100-350 ^{14}C YBP)	0.0067	0.003
	Total	0.0334	0.005

6.1.1 | Early to middle Holocene (c. 10,100–4,000 ^{14}C YBP): Morphological change or stability?

The comparison between early and mid-Holocene foragers revealed differences in both configurations investigated (Figures 4 and 8), especially in the facial module (Figures 5 and 9), which could be interpreted as evidence of biocultural discontinuity but restricted to the beginnings of the middle Holocene (c. 6,000–5,500 ^{14}C YBP). Although the cranial configuration revealed size and shape similarities (Tables 5 and 6) (note the borderline significance of the D^2 distance) between both periods and their average shapes looks similar (Figure 8), there are also differences. For instance, the early/middle Holocene foragers are asymmetrically distributed over the Procrustes shape space corresponding to the PC2 forming two distinct chronological clusters, one of them (inverted triangles along positive scores in Figure 4 and inverted triangles along negative scores in Figure 5) more related to middle Holocene individuals indicating differential affinities between both periods. When EMH and MH samples were compared separately (Figures 6 and 7), differences emerged indicating both that they are more different than it

appears and that the large craniofacial shape divergence occurring during the final late Holocene likely overshadows such differentiation. Early and middle Holocene foragers have different variants of a generalized cranial shape pattern exhibiting longer and narrower cranial vaults, lower and projecting faces and relatively high orbital and nasal apertures. The R-matrix analysis revealed greater than expected phenotypic variances during the early and middle Holocene indicating that the morphological differences viewed between both periods are likely related to gene flow (Tables 7 and 8). Noticeably, the MH sample presented the highest distance to the centroid (r_{ii}) suggesting that a strong genetic divergence occurred during that time. Taken together, these results suggest that the phenotypic differentiation viewed during the first half of the Holocene, although not as strong as that observed later, is related to evolutionary diversification rather than morphological stability. This dynamic scenario coincides with fluctuations in temperature, rainfall and aridity (Mayewski et al., 2004; van der Hammen and Hooghiemstra, 1995) which may have had the potential to cause significant ecological modifications resulting from climate-dependent chorological changes differentially affecting the forager societies, hence promoting population changes (demographic contraction, dispersals, etc).

The beginning of the middle Holocene was a complicated period because evidence of groups with distinct biocultural traits, including mortuary practices (i.e., burial concentration and distribution), lithic

TABLE 8 Analysis of within-group phenotypic variance among diachronic samples investigated

Landmark configuration	Group	Distance to the centroid	Observed variance	Expected variance	Residual variance
Cranial	EMH	0.0363	1.047	0.920	0.127
	MH	0.0639	1.057	0.894	0.163
	ILH	0.0356	1.061	0.921	0.140
	FLHEM	0.0332	0.768	0.923	−0.155
	FLHLM	0.0477	0.780	0.910	−0.130
Facial	EMH	0.0141	1.195	0.954	0.241
	MH	0.0606	1.039	0.909	0.130
	ILH	0.0232	1.103	0.945	0.157
	FLHEM	0.0280	0.747	0.941	−0.194
	FLHLM	0.0453	0.774	0.924	−0.150

Note. Cranial F_{ST} = 0.0522; facial F_{ST} = 0.0334.

TABLE 9 Results of the regression analysis of within- and among- population variance/covariance (V/CV) matrices

Landmark configuration	β	97.5% lower and upper confidence intervals		Adjusted R^2	P value
		Uncorrected variables			
Cranial	0.881	0.790	0.972	0.899	**.0097**
Facial	0.738	0.677	0.800	0.898	**.0091**
		Corrected variables			
Cranial	0.872	0.794	0.950	0.918	**.0052**
Facial	0.736	0.679	0.793	0.911	**.0063**

Note. **In bold** significant *p*-values.

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DELGADO

artifacts for plant processing (anvils, scrapers, hammerstones, among others) and craniodental morphology, appeared in the local archaeological record (Ardila, 1984; Correal, 1990; Delgado, 2012, 2015; Rodríguez Flórez & Colantonio, 2015). Archaeobotanical evidence dated around 5,000/4,000 ^{14}C YBP suggests that certain cultigens, such as squash (*Curcubitapepo*), oca (*Oxalis tuberosa*), Chuguacá (*Hyeronymamacrocarpa*) and *Dioscorea* were introduced during this period (Ardila, 1984; Cárdenas, 2002; Correal, 1990). In addition, during this same time span there is evidence of environmental shifts, that is, an increase in temperature ($\pm$ 2°C) and aridity, reduction of the water tables and Andean forest reduction/fragmentation (Gómez et al., 2007; Marchant et al., 2002; Vélez et al., 2006) coincident with a significant reduction in the archaeological signal (Delgado, 2012). Previously, these events and evidence, from an evolutionary geography perspective (*sensu* Lahr and Foley, 1998), were interpreted as evidence of contraction/extinction of the local foragers likely related with environmental instability *c.* 7,000–6,500 ^{14}C YBP followed by the entry of extraregional populations, coincident with some climatic amelioration *c.* 6,500–5,500[14]C YBP, who by the end of the middle Holocene *c.* 4,000 ^{14}C YBP were already strongly impacting the local gene pool (Delgado, 2012, 2015). The results presented here tend to support rather than contradict such a scenario, as they reveal craniofacial shape divergence between human populations from the early and middle Holocene. Alternatively, the observed morphological diversification could reflect variations in ecology and diet as other investigators have suggested (Rodríguez, 2001, 2007; Rodríguez & Vargas, 2010). However, the SB is not a heterogeneous region with large ecological diversity to generate spatially-driven evolutionary diversification just as it has been showed in other South American regions (Menéndez, Bernal, Novellino, & Perez, 2014; Perez & Monteiro, 2009). Isotopic and bioarchaeological analysis indicated no major dietary shifts between early and middle Holocene foragers, which presented similar patterns of dental wear and oral pathology and shared a similar dietary profile integrated mainly by C_3 resources (plants and animal protein) (Cárdenas, 2002; Delgado, 2016; Gómez, 2012). Interestingly, the isotopic record during the early/middle Holocene (*c.* 7,000 ^{14}C YBP) showed individuals with mixed C_3/C_4 diets supporting the hypothesis of the arrival of groups from the tropical lowlands (Delgado, 2016). Accordingly, the craniofacial shape differentiation observed between early and middle Holocene hunter-gatherers, in agreement with the archaeological evidence and previous bioarchaeological analyses (Ardila, 1984; Cárdenas, 2002; Correal, 1990; Delgado, 2012, 2015), was interpreted as evidence of a process of population change related to the entry of foreign groups toward the beginnings of the middle Holocene.

6.1.2 | Major period of change I Middle to initial late Holocene transition (*c.* 4,000–3,200 ^{14}C YBP)

For the present discussion, more interesting is the craniofacial divergence evidenced around the initial late Holocene (*c.* 3,500 ^{14}C YBP) which stresses a cranial pattern that includes more globular cranial vaults as well as low and projected faces. Size and shape modifications appeared distributed over the entire skull (see Figures 4 and 5) and are significantly different from those viewed among early and mid-

Holocene hunter-gatherers (see Figures 8 and 9 and Tables 5 and 6). Such changes may be indicative of the presence of human populations with distinct craniofacial morphologies or alternatively can be associated with subsistence changes, because from this period onward horticulture and subsequently agriculture becomes the main economic strategy.

The isotopic record shows that during this time span people presented different dietary patterns (C_3, mixed C_3/C_4 and C_4), but without a clear trend toward C_4 plants (Cárdenas, 2002; Delgado, 2016; Delgado, Langebaek, Aristizabal, Tykot, & Johnson, 2014; van der Hammen et al., 1990). This is supported for the diverse archaeobotanical record that includes sweet potato (*Ipomoea batata*), calabash tree (*Cresentia cujete*), avocado (*Persea americana*), cherry-tree (*Prunos serotina*), and maize (grains and cobs of *Zea mays*) (Correal, 1990; Correal & Pinto, 1983). The lack of strong evidence of C_4 plants (i.e., maize) during the initial late Holocene (*c.* 3,500 ^{14}C YBP) is striking because according to local archaeologists the high frequency of this and other tropical plants is an indisputable marker of agriculture (Botiva, 1989; Correal, 1990; Correal & van der Hammen, 1977). Importantly, the bioarchaeological record does not support a substantial subsistence transformation because the frequencies of oral pathology remain relatively the same regarding the MH, although a slight decrease in the occlusal surface wear has been pointed out (Delgado, 2015). In addition, although food-processing lithic tools were found in strata dated *c.* 5,000 ^{14}C YBP and C_3 plants early cultivation likely started *c.* 5,000/ 4,000 ^{14}C YBP, the evidence of a strong dependence of cultivated crops, according to the isotopic and archaebotanical record, did not occur during the initial late Holocene, but during the final late Holocene (Cárdenas, 2002; Correal, 1990; Correal & Pinto, 1983; Delgado, 2016). Therefore, the pattern and magnitude of the observed cranial divergence cannot be related to adaptations in response to the adoption of agriculture, because the most dietary transformation occurred later coincident with the strongest phenotypic diversification. Conversely, gene flow becomes the most likely driver of morphological change during the initial late Holocene. Climatic-driven morphological divergence can be ruled out since the late Holocene (the last 4,000/ 3,500 years) is a period with relative environmental stability with minor fluctuations in humidity and dryness (Marchant et al., 2002; Mora & Pratt, 2002).

A major concern in the local prehistory is whether the tropical crop horticulture was introduced via population dispersals or cultural contacts (Botiva, 1989; Correal & Pinto, 1983). The archaeological record suggests that the introduction of maize horticulture coincides with the first appearance of ceramic technology in the region (Correal, 1990; Correal & Pinto, 1983). This evidence along with the craniofacial change here evidenced, suggest that the extensive biocultural change observed during this time frame is concordant with the arrival of extraregional populations. This is supported by the analysis of differential gene flow (Tables 7 and 8) which showed that the regional F_{ST} value increased when the ILH sample was included and its positive residual within-group variance suggest that populations inhabiting the region during that time experienced greater than average extraregional gene

flow. The investigation of other skeletal traits (craniometric and dental measurements as well as cranial and dental nonmetric variants) exhibit the same picture, that is, phenotypic differentiation during the initial late Holocene, indicating that effectively new morphologies appeared during that time (Delgado, 2015; Rodríguez Flórez & Colantonio, 2015). Unfortunately, skeletal samples with similar chronologies outside the SB region are extremely scarce to evaluate the geographic origin of the arriving populations. In contrast, the archaeological and isotopic record suggest that the most probable source region of such populations is the tropical Middle Magdalena valley (Cárdenas, 2002; Correal, 1990; Correal & van der Hammen, 1977; Delgado, 2015).

The magnitude of the population event that occurred during the initial late Holocene is difficult to be established, especially given the paucity of the skeletal record. However, taking into account that an extensive craniofacial diversification did not occur (Figures 4–8, and 9) and that there was an increase in biological diversity during this time (Table 7), we may speculate that the change observed is more in agreement with a demic expansion of farming populations from the Middle Magdalena valley. Under this hypothesis, the pre-existing populations were not replaced, but partially assimilated, increasing the biological diversity and the new economic, technological, and sociocultural traits introduced were rapidly scattered through the region.

6.1.3 | Major period of change II Final late Holocene (c. 2,000/1,500 ^{14}C YBP)

The results presented revealed a transformation of the skull morphology during the final late Holocene (c. 2,000/1,500 ^{14}C YBP). Distinct from the previous periods, the R-matrix analysis indicates loss of diversity (very low F_{ST} values and negative residual variance as seen in Tables 7 and 8). Therefore, according to the model, genetic drift rather than gene flow better explains the reduction of biological diversity. However, because the SB populations reached the highest population size during the Muisca period, the action of genetic drift is unlikely. According to the beta test (Table 9), the sole action of random evolutionary factors does not explain the morphological divergence observed, hence, natural selection and/or phenotypic plasticity become important as potential diversifying sources.

According to the archaeobotanical and isotopic record during the final late Holocene, the SB populations presented a distinct dietary pattern composed of several cultigens relying heavily on C_4 plants (i.e., maize) (Cárdenas, 2002; Delgado, 2016). In addition, the archaeological evidence suggests that food processing technologies (pottery and grinding tools) were widespread and intensively used in the region (Boada, 2007; Botiva, 1989; Langebaek, 1995). Those changes were accompanied, as revealed by several bioarchaeological indicators, by a general decline in health along with reduction in nutrition quality and in dietary diversity (Delgado, 2015, 2016; Delgado et al., 2014; Martínez, 2012). This suggests that SB populations experienced a major biocultural shift during this time that includes, among other things, very high consumption of highly processed rich-carbohydrate food-stuffs (García, 2012). This is relevant because several studies have suggested that changing diets are among the most relevant ecological factors shaping the patterns of human craniofacial variation, because distinct food

types influence growth of the skull during the late ontogeny, both by their nutritional proprieties and by mechanical loading from mastication (Carlson & van Gerven, 1977; Collard & Wood, 2007; Lieberman, Krovitz, Yates, Devlin, & St. Claire, 2004; Menéndez et al., 2014; Noback & Harvati, 2015a, 2015b; Paschetta et al., 2010; Perez et al., 2011; von Cramon-Taubadel, 2011). The multivariate exploratory techniques showed shape changes across the skull both in cranial vault/base and face but mostly in the masticatory complex (maxilla, zygomatics, etc) (Figures 4–8, and 9). Additionally, the cranial and facial size fluctuations during this time suggest covariation between size and shape in response to external factors (Figure 3). Those size and shape changes configure a cranial pattern characterized by shorter and wider cranial vaults, wider and more retracted faces and large orbital and nasal apertures. The emergence of this pattern called by some researchers as "Amerindian or derived" (Neves et al., 2007) has been previously attributed to masticatory adaptations related to subsistence changes (Larsen, 1997). Larsen (1997) discusses the shift in craniofacial morphology concomitant with changes in dietary behavior; namely, decreased robusticity and cranial length, accompanied by an overall increase in cranial height. In the same vein, recently, von Cramon-Taubadel (2011) and Noback and Harvati (2015a, 2015b) stressed the importance of subsistence strategy as one of the main ecological factors underlying the evolution of modern human cranial variation. Importantly, the last authors suggested that morphological shifts promoted by dietary adaptations occur in distinct cranial regions not necessarily related to the masticatory complex, but in the cranial vault and base, which is explained by the integrative nature of the human skull. Thus, selection and/or phenotypic plasticity acting on relatively integrated structures can produce modifications jointly in several cranial regions (Lieberman, 2011; Martínez-Abadías et al., 2012; Smith, 2011; von Cramon-Taubadel, 2011). This suggests that the transformation observed toward a derived cranial pattern in the study region is likely related to the action of directional factors in response to an important reduction in the masticatory forces and homogenization of diet. Neither stabilizing nor diversifying selection explains the large change observed, because there is no evidence that supports negligible morphological divergence or the existence of at least two distinct cranial patterns representing the extremes of the phenotypic spectrum. Randomly fluctuating selection does not seem to be an important force because several independent factors apparently did not influenced the morphological change. In contrast, directional selection and/or phenotypic plasticity may account for the change viewed because a distinct and widespread phenotypic pattern emerged, likely influenced by just one factor (i.e., diet). Phenotypic plasticity is thought to be one of the most important drivers of morphological diversification over short evolutionary time scales in human populations that experienced a recent divergence (i.e., a recent subdivision from an ancestor), changes in diet and increase in population size (Menéndez et al., 2014; Perez & Monteiro, 2009). However, directional selection can also act at microevolutionary scales causing rapid and dramatic shape changes in one direction, occasionally promoting correlated morphological evolution (Grant & Grant, 1995; Melo & Marroig, 2015; Polly, 2004). Here, the action of both directional selection and phenotypic plasticity may

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have played an important role, given the large craniofacial divergence observed and the apparently correlated evolution of distinct cranial components.

Finally, the hypothesis of a major role of directional factors shaping the pattern of craniofacial variation during the final late Holocene must be viewed in the context of population continuity. This disagrees with the most accepted view for the late Holocene population history of the SB which suggests that the important differences in population size, agricultural and technological development, and sociopolitical complexity between the Herrera and Muisca periods involved two different source populations (Botiva, 1989; Langebaek, 1995). The results presented here can also support the alternative hypothesis, that is, the craniofacial differences between Herrera and Muisca populations are related to the action of directional evolutionary processes and not necessarily to the arrival of new populations. Recent archaeological research indicated that in several sites there is no evidence of a cultural change, but continuity in numerous cultural traits (e.g., settlement patterns, ceramic styles, etc) (Boada, 2007). Interestingly, the study of other phenotypic traits, including dental and cranial nonmetric characters, revealed close biological affinities between Herrera and Muisca samples (Delgado, 2015; Delgado, Scott, & Turner, 2010). Together this evidence suggests a distinct interpretation for the final late Holocene population history of the SB region where the Herrera horticulturalists were not replaced by foreign populations, but evolved into intensive agriculturalists (*c*. 3,000–2,000 ^{14}C YBP).Therefore, the strong biocultural change observed during the -Herrera to Muisca transition- is the result of both the action of natural selection/phenotypic plasticity as well as the existence of extensive cultural contacts and broad commercial networks.

7 | CONCLUDING REMARKS

7.1 | Past interpretations and current evidence on the SB population history

Addressing the population history and specifically the biocultural continuity/discontinuity by means of the archaeological and bioarchaeological record is not an easy task and depends on several factors including the temporal and spatial scale of analysis and the types of evidence included. Here, biocultural in the sense of Barrientos (2009, p. 193) refers to the variation in the two large components of the human phenotype—systemically related but distinguishable—the structural-morphological-physiological and the behavioral-cultural. Following Ames (2000), the behavioral-cultural discontinuity refers both to the cessation in the transition of one or more traits detectable along a cultural tradition and as the presence of interruptions in the chain of evidence. In the same way, according to Barrientos (2009, p. 194), the structural-morphological-physiological- discontinuity implicate the existence of interruptions in the transmission of genetic-epigenetic information related to the local or total extinction of the involved community of reproduction either a lineage, population or species. In the present case, both notions of discontinuity may be involved. According to some authors (Correal & van der Hammen, 1977; Neves et al., 2007; Rodríguez, 2001, 2007; Rodríguez & Vargas, 2010; van der

Hammen et al., 1990), the main arguments favoring the alleged population continuity are: (i) the persistence of the Abriense lithic tradition over time, (ii) the gradual transformation of the subsistence systems, and (iii) the alleged temporal stability of craniofacial morphology. However, the finding of distinct lithic tools morphofunctionally unrelated to the Abriense industry contradicts its "ubiquitous nature" 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. Thus, the Abriense tradition presents remarkable discontinuities over the Holocene, which are reflecting population/cultural change rather than *in situ* evolution. Regarding the second notion of discontinuity, there exist clear interruptions in the chain of evidence as viewed from temporal sequences of stable isotopes, radiocarbon dates and diachronic morphological variation. As shown above and elsewhere (Cárdenas, 2002; Delgado, 2016; Delgado et al., 2014), there is not a strict long and gradual dietary transformation in the region, but relatively important fluctuations during the early mid-Holocene and especially during the initial late Holocene, which does not support a major temporal stability in diet and subsistence and stresses the role of population contacts promoting some economic changes. Similarly, when the available regional radiocarbon data base was analyzed (Delgado, 2012, 2015), several gaps coincident with some rapid climatic change periods (Mayewski et al., 2004) were detected which support the idea that the decreasing archaeological signal during such periods is better explained by the occurrence of contraction/extinction of the local populations and the subsequent entry of extraregional groups from different geographical sources (Delgado, 2012, 2015). The study of the craniofacial shape divergence here presented along with other phenotypic evidence (Delgado, 2012, 2015, Rodríguez Flórez & Colantonio, 2015) revealed important morphological diversification over the Holocene, implying both population contacts and adaptations. The extensive evidence presented here disagrees with the traditional and simplistic view of a long-standing biological continuity without major evolutionary and population changes (contra Rodríguez, 2001, 2007; Rodríguez & Vargas, 2010). Instead it supports a complex population history scenario where population contractions, extinctions, dispersals and assimilations along with dietary adaptations took place during the last 10,000 years of human evolution in the SB region.

Lastly, the discontinuity scenario here outlined deserves further investigation, perhaps with more detailed evidence such as 3D craniodental morphology and ancient DNA especially given the availability of well-preserved human skeletons with good archaeological and chronological contexts that encompass the whole Holocene period.

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