The interaction of neutral evolutionary processes with climatically-driven adaptive changes in the 3D shape of the human os coxae

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Abstract

Differences in the breadth of the pelvis among modern human populations and between extinct hominin species have often been interpreted in the light of thermoregulatory adaptation, whereby a larger pelvic girdle would help preserve body temperature in cold environments while a narrower one would help dissipate heat in tropical climates. There is, however, a theoretical problem in interpreting a pattern of variation as evidence of selection without first accounting for the effects of neutral evolutionary processes (i.e. mutation, genetic drift and migration). Here, we analyze 3D configurations of 27 landmarks on the os coxae of 1,494 modern human individuals (922 males and 572 females) representing 30 male and 23 female populations from five continents and a range of climatic conditions. We test for the effects of climate on the size and shape of the pelvic bone, while explicitly accounting for population history (i.e. geographically-mediated gene flow and genetic drift). We find that neutral processes account for a substantial proportion of shape variance in the human os coxae in both sexes. Beyond the neutral pattern due to population history, temperature is a significant predictor of shape and size variation in the os coxae, at least in males. The effect of climate on the shape of the pelvic bone, however, is comparatively limited, explaining only a small percentage of shape variation in males and females. In accordance with previous hypotheses, the size of the os coxae tends to increase with decreasing temperature, although the significance of the association is reduced when population history is taken into account. In conclusion, the shape and size of the human os coxae reflect both neutral evolutionary processes and climatically-driven adaptive changes. Neutral processes have a substantial effect on pelvic variation, suggesting such factors will need to be taken into account in future studies of human and fossil hominin coxal variation.

Keywords: pelvis; neutral variation; selection; climate; os coxae

Introduction

The human pelvis is a key anatomical region in studies of human evolution, given its direct involvement in obligatory bipedal locomotion and parturition of a remarkably encephalized neonate, both characteristics of the hominin lineage (Krogman, 1951; Rosenberg, 1992; Rosenberg and Trevathan, 1995; Weaver and Hublin, 2009; DeSilva, 2011). When compared with other hominoids, or more widely to other catarrhines, the shape of the human pelvis is markedly distinct (e.g., Schultz, 1936; McHenry and Corruccini, 1978; Lovejoy, 1988; Lycett and von Cramon-Taubadel, 2013). The human os coxae, in particular, is morphologically more different from closely related species such as chimpanzees (genus *Pan*) or gorillas (genus *Gorilla*), than far more phylogenetically distant catarrhine species are from each other (Lycett and von Cramon-Taubadel, 2013). Such a substantial morphological divergence between humans and other apes, attained in the relatively short period of time since divergence from the last common ancestor, suggests that strong selective processes have acted on the pelvic girdle (Grabowski et al., 2011; Grabowski, 2012).

Adaptation to bipedal locomotion has been often suggested as the ultimate driving factor that led to our distinct pelvic shape (Straus, 1929; Waterman, 1929; Reynolds, 1931; Schultz, 1936; Berge, 1984; Ward, 2002). The ever increasing fossil record suggests that an efficient bipedal locomotion was achieved in our lineage well before the origin of the genus *Homo*, at least by australopithecine species (e.g., Lovejoy et al., 1973; Marchal, 2000; Lovejoy, 2005; Lovejoy et al., 2009; DeSilva et al., 2013), with a major rearrangement of the pelvic girdle that accompanied the shift to this new form of locomotion.

Humans are also distinct from other primates in having a relative large brain in respect to body size. The obstetrical requirements for a spacious birth canal, necessary to allow the passage of the unusually encephalized human neonate, have been suggested to conflict with the requirements for an efficient bipedal gait, which privileges a shorter and narrower pelvis (Lovejoy et al., 1973; Tague and Lovejoy, 1986; Tague, 1991; Häusler and Schmid, 1995; Rosenberg and Trevathan, 1995; Ruff, 1995; Trevathan and Rosenberg, 2000; Lovejoy, 2005; Simpson et al., 2008; Kibii et al., 2011; but see Dunsworth et al., 2012). The result of the two opposing selective forces led to a particularly close fit between the size of the neonate and pelvic canal dimensions, which is sometimes the cause of complications during parturition (Schultz, 1949; Leutenegger, 1974; Rosenberg, 1992; Trevathan and Rosenberg, 2000; DeSilva, 2011).

Beyond these two important selective pressures, thermoregulatory adaptations to different climates have also been proposed as important factors in shaping the pelvis of extinct hominins and modern humans (Ruff, 1993, 1994, 1995; Holliday, 1997b; Weaver and Hublin, 2009; Holliday and Hilton, 2010). On the basis of multiple lines of evidence, it is now widely accepted that the species *Homo sapiens* evolved in sub-Saharan Africa within what was essentially a tropical climatic zone (Cann et al., 1987; Ingman et al., 2000; Thomson et al., 2000; McDougall et al., 2005; Henn et al., 2012; Manica at al., 2007; Weaver, 2012). However, following a period of global expansion occurring within a timeframe of approximately ~50 KYRs (Eriksson et al., 2012), our species subsequently came to permanently inhabit every continent with the exception of Antarctica, adapting to a wide variety of climatic conditions.

Differences in body size and proportions between populations or closely related species of endotherms living in different climatic regions have been recognized since the end of the 19th century. These biogeographic patterns are usually referred to as Bergmann's and Allen's "rules". Following Bergmann's (1847) rule, endotherms living in colder environments tend to have larger bodies than closely related species inhabiting warmer regions. An increase in body size maintaining a similar shape results in a lower surface-to-volume ratio, and given that endotherms generate heat internally and dissipate it at the surface, a lower ratio can help preserve body temperature in cold climates. Allen's (1877) rule, on a similar line, suggests that the relatively shorter extremities (ears, limbs and tail) displayed by cold-adapted endotherms are advantageous because they tend to have a lower surface-to-volume ratio and a relatively lower rate of heat dissipation than longer extremities.

Both Allen's and Bergmann's rule have been used to explain differences in body size and body proportions in modern human populations, with high-latitude populations showing larger body size and relatively shorter limbs than tropical populations (Schreider, 1950; Newman, 1953; Roberts, 1953; Baker, 1960; Newman, 1961; Coon, 1962; Schreider, 1964, 1975; Roberts, 1978; Crognier, 1981; Ruff, 1994; Holliday, 1997a, b; Katzmarzyk and Leonard, 1998; Holliday, 1999, 2002; Ruff, 2002; Weaver, 2002; Weaver and Steudel-Numbers, 2005; Weinstein, 2005; Tilkens et al., 2007; Weaver and Hublin, 2009). The presence of these biogeographic patterns in modern humans implies that similar adaptive responses could have been developed in other hominins. Differences in body proportions and body robusticity between and within extinct hominin species, particularly between higher-latitude Neanderthals and coeval tropical-adapted modern humans, have been often interpreted in the light of thermoregulatory efficiency (Trinkaus, 1981; Ruff, 1991, 1993, 1994; Holliday, 1997a,b; Pearson, 2000; Weaver, 2003; Weaver and Steudel-Numbers, 2005; Weaver, 2009). Climatic adaptation has also been indicated as a key factor in constraining the evolution of the pelvis in our lineage, limiting the scope of adaptive changes related to locomotory and obstetrical selective pressures (Ruff, 1995; Weaver and Hublin, 2009).

In regard to modern pelvic variation, bi-iliac breadth has been shown to be larger in high-latitude human populations than in tropical areas (Ruff, 1991, 1994, 2002; Weaver, 2002; Holliday and Hilton, 2010; Auerbach, 2012; Cowgill et al., 2012; Kurki, 2013). Ruff (1991, 1994) developed a cylindrical model of the human body in order to directly relate changes in body breadth with the thermoregulatory principles underlying Bergmann's rule. The model approximates the human body to a cylinder whose height is given by the body stature and whose breadth (diameter) can be approximated using pelvic bi-iliac breadth. One important property of a cylinder is that the ratio between surface area and volume does not change by altering the cylinder height, but altering only its diameter, with wider cylinders always associated with a lower surface-to-volume ratio. In accordance with this model, absolute pelvic breadth, independently of stature, would be a strong determinant of the aptitude to dissipate body heat in hot regions, and to preserve it in cold environments. Ruff (1994) showed that the expectations of the model are met in human populations, with populations living at low latitudes having an absolutely narrower body (bi-iliac) breadth than populations from high latitude regions, while stature showed no significant correlation with latitude and, therefore, temperature.

Following an analogous reasoning, differences between Neanderthal and modern human pelvic breadth and shape could derive from adaptation to cold-temperate climates and tropical climates, respectively. Neanderthals lived through several glacial cycles in the higher latitudes of Europe, where hypothermia could have been a substantial selection pressure. Conversely, modern humans evolved in generally warmer Africa, where selection likely favored adaptations to mitigate heat-stress, and expanded into high-latitude regions only after about 50kya (e.g., Eriksson et al., 2012). The two species share the same mode of locomotion, and have been suggested to experience similar obstetrical difficulties due to a close correlation between the size of the birth canal and that of the newborn (e.g., Rosenberg et al., 1988; Tague, 1992; Ponce de León et al., 2008; Franciscus, 2009; Weaver and Hublin, 2009). Considering their adaptation to different climates, thermoregulatory factors have been proposed to explain the wider Neanderthal pelvis in respect to most anatomically modern humans (Ruff, 1994, 1995; Holliday, 1997a; Weaver, 2009; Weaver and Hublin, 2009).

Although such adaptive explanations are certainly viable, there is a major theoretical problem with interpreting an empirical correlation between climate and pelvic breadth as being equivalent to the causative effect of climatic selection, without first controlling for the underlying pattern of phylogenetic relationships (Felsenstein, 1985; Martins and Hansen, 1997; Nunn and Barton, 2001). Moreover, Ackermann and colleagues (Ackermann and Cheverud, 2004; Ackermann and Smith, 2007) have suggested that morphological diversity patterns observed in the hominin fossil record, even between taxa classified as different species or even genera, might be explained on the basis of neutral evolutionary processes such as genetic drift, without the need to invoke a selective explanation. It has recently been suggested that modern human pelvic shape diversity reflects neutral population history, carrying the signature of the serial founder events that accompanied the expansion of our species out of Africa (Betti et al., 2012, 2013), as it was previously shown for cranial diversity (Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009). Similarly, when examining pelvic differences between modern populations, we might expect that shared population history and gene flow would have generated a pattern of genetic and morphological similarity between populations that needs to be explicitly taken into account before testing the effect of any proposed selective factor. In other words, the underlying neutral pattern of variation due to population history should represent the null hypothesis against which to test the effect of additional, non-neutral processes (Roseman and Weaver, 2007).

It is arguably more difficult to judge the relative importance of selective and neutral processes in extinct hominins, due to our limited understanding of within-taxon variation, patterns of sexual dimorphism and the large temporal scales involved (Ackermann and Smith, 2007). On the other hand, disentangling the effects of climate and population history in our species, which spans the most extreme climates and is represented by a large number of skeletal remains in osteological collections worldwide, can help us understand the relative importance of climatic adaptation and neutral processes in shaping the pelvis, at least in one hominin. Given that *Homo sapiens* is the only extant hominin species, it represents the most appropriate model for investigating evolutionary processes in extinct (bipedal) hominins. Using modern human populations has the additional advantage that we can test for climatic adaptation on the pelvis without the confounding effect of other evolutionary factors, such as locomotory adaptation and obstetric requirements, which are similar, if not identical, in all human populations.

Aims and objectives

Taking advantage of the large number of human skeletal remains stored in several museum and university collections, we compiled a large global dataset of three-dimensional landmark configurations of the human os coxae (n = 1,494 individuals), in order to gain a representative view of pelvic bone variation in our species. In order to enable tests for the effects of both neutral patterns of pelvic bone variation and climate-related differences, the dataset (see below) was specifically built to include populations of different ancestry and geographic provenance, consequently spanning a wide range of climatic conditions.

The current model of climatic adaptation of the human pelvis is based primarily on pelvic breadth, which is measured as the maximum distance between the lateral margin of the right and left iliac crests in the fully articulated pelvis. While this measurement captures an approximation of body breadth, it does not allow clear discrimination between size and shape variation in the human pelvis. Indeed, a large pelvic breadth could be due to an isometric increase in size in the three bones that form the pelvic girdle (i.e. the sacrum and the ossa coxae), as expected under Bergmann's rule, or by a change in shape of the bones which in turn affects the dimensions of the articulated structure.

The aims of this study can be summarized as follows:

1) To reaffirm the effect of neutral evolutionary processes (i.e. genetic drift and migration) in determining human pelvic bone shape variation across populations.

2) To evaluate the effect of climatic adaptation on the size and shape of the os coxae while accounting for the underlying neutral pattern of population history.

Materials and methods

Materials

Morphometric data of the os coxae were collected by one of us (LB) for 1,494 individuals, 922 males and 572 females, representing 30 male and 23 female populations from five continents and a wide variety of climatic conditions (Table 1, Figure 1). The minimum sample size for the populations is 8 individuals, with an average sample size of 30.7 and 24.9 individuals for males and females, respectively. Males and females were separated in all analyses, as the two sexes show substantially different coxal shape patterns, most likely due to female-specific evolutionary constraints related to parturition (e.g., Schultz, 1949; Leutenegger, 1974; Rosenberg and Trevathan, 1995; Correia et al., 2005; Weaver and Hublin, 2009).

Exclusively adult individuals were included in the study, defined as individuals whose iliac crest was completely fused. Determination of sex, when not recorded at the death of the individual, was performed using standard non-metric methods (Phenice, 1969; Işcan and Derrick, 1984; Sutherland and Suchey, 1991). Accuracy of sex assessment was estimated as in Betti et al. (2013), by using a subset of individuals of known sex, representing different continents, to derive a sex discriminant function. The function was then applied to two other subsets of individuals, one of known- and one of unknown-sex. The application of the discriminant function to the unknown-sex subset returned the same results of the visual determination in 98.2% of the cases. A similar percentage of matching results (98.8%) was obtained for the known-sex subset, therefore supporting the accuracy of visual sex assessment (Table S1).

The complex three-dimensional shape of the os coxae is not easily captured by linear measurements (McHenry and Corruccini, 1978); therefore, we adopted a geometric morphometric approach, selecting a set of 27 landmarks (Figure 2, Betti et al., 2013) measured using an Immersion 3D Microscribe digitizer. The data were collected unilaterally, on the best preserved (i.e. most complete) os coxae. Prior to formal data collection, intra-observer repeatability was tested by performing five repeat measurements of all landmarks on three ossa coxae from different individuals, one female and two males. Landmarks with standard deviations under 1 mm were deemed repeatable, following von Cramon-Taubadel et al. (2007). Differences in position, rotation and size between individual configurations were corrected by generalized Procrustes superimposition (Gower, 1975; Rohlf, 1990; Rohlf and Slice, 1990; Rohlf and Marcus, 1993) in Morphologika 2.5 (O'Higgins and Jones, 1998), in males and females separately. After Procrustes superimposition, centroid sizes for individual configurations were retrieved and used as an indicator of size of the os coxae, and shape and size data were analyzed separately. New morphometric variables were extracted from the whole 3D configuration of the os coxae by performing a Principal Component Analysis (PCA) in Morphologika on the covariance matrix of the Procrustes coordinates (as projected on the tangent space). The obtained PC scores, representing 100% of the total shape variance, were used as morphometric data in the shape analyses.

Climatic data (average minimum temperature of the coldest month, average maximum temperature of the hottest month and average annual precipitation) were obtained from WorldClim (http://www.worldclim.org/), as interpolated GIS layers with 30 arc-second definition (ca. 1 km) (Hijmans et al., 2005). The data are reported in Table S2.

Estimating the signature of neutral population history on shape differences

The correlation between genetic and geographic distance has been shown to be strong in human populations (Relethford, 2004b; Manica et al., 2005; Lawson Handley et al., 2007; Romero et al., 2008).

This empirical relationship is due to the combined effects of the expansion of our species into new continents (i.e., out-of-Africa dispersal), so that geographically closer populations tend to share a more recent common ancestor, historical long range migrations and on-going gene flow between populations. These demographic processes are mediated by geographic distance, explaining the overall correlation between genetic and geographic distance. On this basis, geographic distance has been used successfully as a proxy for genetic distance in several studies of human phenotypic variation for which no genetic data were available (e.g., Relethford, 2004a, 2009; Betti et al., 2010). In this paper, the signature of past population history, reflected in the relationship between geographic and phenotypic distance between populations, will be referred to as the demographic history signature (DHS). Due to the empirical nature of this relationship and the lack of a model that accounts for all demographic processes acting in our species, both a linear and a non-linear relationship between phenotypic and geographic distance (the latter a proxy for genetic distance) will be used here to quantify the relative effect of neutral population history on morphometric differences between populations.

Between-population morphometric distances were calculated following Relethford and Blangero (1990) and Relethford et al. (1997), using the software R version 3.0.0 (R Core Team, 2013). The Relethford-Blangero method explicitly models morphometric data as quantitative traits and derives a matrix of genetic distances (**Q**) from the pooled within-population phenotypic covariance matrices scaled on the traits' heritability (h^2). In the absence of specific knowledge of traits heritability, we used total heritability ($h^2 = 1$), therefore assuming equivalence between the phenotypic and the additive genetic covariance matrices, an approximation that is supported by the proportionality of the two matrices, as suggested by previous studies (e.g., Cheverud, 1988; González-José et al., 2004). The Relethford-Blangero method usually requires a z-score correction of the raw data in order to remove differences in scale between traits. However, coordinate data do not present differences in scale and, therefore, no z-score correction was used in this study. This decision does not impact the results in any way, given that the correction would not affect the estimated distance matrix between populations. We corrected the phenotypic covariance matrices for sample size, as suggested by Relethford et al. (1997). Since phenotypic distances between populations included in the **Q** matrix are effectively ratios, the distance matrix was normalized using an arcsine square root transformation (Storz, 2002; Roseman and Weaver, 2004; Betti et al., 2010).

Pair-wise population geographic distances (**D**) were calculated as the shortest routes across landmasses, avoiding areas with a mean altitude higher than 2,000 m over sea level (Manica et al., 2005; Prugnolle et al., 2005). Connections between Eurasia and America assumed a land bridge on the Bering Strait, and additional land bridges were also assumed between the Malay Peninsula and Australia, through the major Indonesian islands.

The fit to the DHS was tested using a non-linear model as well as a linear relationship with geographic distance. The linear approximation uses a simple Mantel test (Mantel, 1967) to test for significant correlation between phenotypic (**Q**) and geographic (**D**) distance. The Mantel test was performed with the software R, using the package *vegan*, with 10,000 randomization cycles. A more realistic non-linear model was developed using a spline model in R (function *smooth.spline*, penalty = 4), whose flexibility allows to better capture the empirical relationship between geographic and phenotypic distance. A penalty of four was chosen in order to reduce the complexity of the curve while maintaining a good fit with the data. The significance of the fit, measured as the proportion of explained variance (R^2), was tested using a randomization approach similar to the one employed in Mantel tests.

Testing for the effect of climate on the size of the os coxae

Average coxal (centroid) size for each population was regressed on the three climatic variables (minimum temperature, maximum temperature and precipitation). In order to account for the fact that geographically closer populations are expected to be more similar to each other due to shared population history and gene flow, spatial autocorrelation was taken into account in the regression model. The regression of coxal size on climate was computed with a Generalized Least Square analysis using the R software (GLS, function gls in library nlme; http://stat.ethz.ch/R-manual/R-patched/library/nlme/html/ gls.html), specifying a spatial autocorrelation structure (Zuur et al., 2009). In order to account for a spatial autocorrelation structure, the GLS algorithm calculates pair-wise geographical distances between populations from spatial coordinate data, computing Euclidean distances between coordinate points. However, overland distances between human populations, corresponding to likely routes of expansion and migration, are effectively non-Euclidean distances. To overcome the problem, Multi Dimensional Scaling (MDS) was applied to the original matrix of overland geographic distance, in order to extract a number of orthogonal axes to be used as new spatial coordinate axes. Five MDS axes were selected and used as spatial coordinate for the GLS analysis. A Mantel test confirmed that original and new distances, calculated from the MDS variables, were highly correlated ($r = 0.998$ and $p < 0.001$ in males, $r = 0.999$ and $p < 0.001$ in females).

Different autocorrelation structures were tested by fitting them to the data in a GLS model, and an ANOVA test was carried out to test the significance of the contribution of each spatial autocorrelation structure to the model. When adding significant improvement, the structure associated with the largest decrease in AIC (Akaike Information Criterion; Akaike, 1973) was chosen for the analyses; a rational quadratic correlation structure appeared to be the best option in most cases.

Testing for the effect of climate on shape differences between populations

Three matrices of climatic distance between populations (**Tmin**, **Tmax** and **Prec**) were computed for minimum temperature, maximum temperature and precipitation as the Euclidean distance between population values.

In order to control for population history, we repeated the analysis by first fitting the non-linear relationship between **Q** and **D**, and then testing for a linear association with the climatic matrices (Betti et al., 2010). Significance was assessed by randomizations (n = 10,000), with one-tailed tests to maximize the power of detecting positive relationships, and the fit was expressed as percentage of explained variance (R^2). The analyses were also performed controlling for the simpler linear relationship between **Q** and **D**, using a partial Mantel test.

The visualization of morphological differences associated with climate was achieved by running a two-blocks Partial Least Square (PLS) analysis (Rohlf and Corti, 2000; Bookstein et al., 2003) in MorphoJ. The analysis identifies the major axes of covariation between shape (the first block, represented by the Procrustes variables) and climate (the second block, represented by the three climatic variables, standardized by z-score transformation). The multivariate morphological changes associated with the main axes of covariation between shape and climate were visualized in Morphologika using 3D wireframes connecting the pelvic landmarks.

Results

Neutral population history: fit between morphological and geographic distance

The results show a significant fit of coxal shape variation to the demographic history signature (DHS), for both sexes. Population differences in coxal shape, in fact, increase sharply with geographic distance until they reach an asymptote at around 7,000km. The pattern is captured by both the simplified linear regression model ($R^2 = 0.130$, $p < 0.001$ in males; $R^2 = 0.106$, $p < 0.001$ in females) and the more realistic non-linear DHS model ($R^2 = 0.345$, $p < 0.001$ in males; $R^2 = 0.306$, $p < 0.001$ in females). Figure 3 shows the fit of the linear and the non-linear model to the data.

Effects of climate on coxal size

The results of the GLS model, regressing average coxal centroid size against the three climatic variables, are reported in Table 2. The table includes the results of the ANOVA test comparing the model with and without spatial autocorrelation (ANOVA p-value; spatial autocorrelation structure = rational quadratic). In all cases, spatial autocorrelation (SAC) is a significant factor when considering the relationship between average coxal size and climatic variables and, therefore, needs to be taken into account. When accounting for SAC, only minimum temperature and precipitation show a significant relationship with coxal size in males, and no significant relationship is found in females (Table 2). In males, larger os coxae are associated with cold temperature and dry conditions, while smaller size is associated with hot and humid climates.

The results show a difference in how coxal size relates to climate in males and females. However, the different results could be due to the smaller female dataset (23 populations instead of the more numerous 30 male populations). To make the datasets for the two sexes directly comparable, the analyses were repeated on 22 populations for which both male and female individuals were available. In addition, to avoid a bias due to a larger male sample size in most populations, the number of individuals in each population was adjusted to the same sample size in both sexes (bringing the dataset to n=536, for males and females). The results of this new analysis confirmed a significant correlation between coxal size and minimum temperature in males exclusively (Table 3).

Effects of climate on coxal shape

Differences in shape among populations are associated with differences in temperature in males and females (Table 4). This association remains significant in males, once corrected for spatial autocorrelation in the form of a non-linear model of the DHS (see Table S3 for analogous results obtained after correcting for a linear model of geographic distance). In females, only the correlation with maximum temperature remains significant after accounting for DHS (Table 4). The analyses were repeated for the 22 populations for which both male and female individuals were available, in order to verify if the differences in the results between the sexes could be due to the smaller number of female population samples (Table 5). The results confirm a difference between the sexes in regard to the effect of climate on coxal shape changes.

Although it is impossible to completely isolate the effects of climate on shape from those of other factors, the changes in morphology that show the highest correlation with climate give an indication of what aspects of shape are potentially associated with temperature and humidity levels. The two-block PLS analysis confirmed a significant, although limited, overall correlation between pelvic shape and climate in both males (RV coefficient = 0.074, $p < 0.001$) and females (RV coefficient = 0.089, $p < 0.001$). The first two axes of covariation (PLS 1 and PLS 2) explain, respectively, 82.9 % and 15.3 % of the covariation between the two blocks of variables in males ($p < 0.001$ for both axes), and 75.9 % and 21.2 % of the covariation in females ($p < 0.001$ for both axes). The correlation between the two blocks is significant for all the PLS axes (Table S4). Only the first two PLS axes will be examined in detail, as they explain the majority of the covariance between shape and climate. Changes in shape along PLS 1 mainly reflect differences in temperature between geographic regions, while changes along PLS 2 reflect differences in precipitation (Table 6). The variation in shape along these two axes is shown in Figure 4. In males and females, low scores of PLS 1 tend to correspond to low temperatures. For PLS 2, low scores correspond to low precipitation in males and high precipitation in females (see Table 6). Shape changes along the PLS axes are subtle, but remarkably similar in males and females, suggesting population-specific rather than sex-specific effects (Figure 4).

Discussion

Differences in pelvic breadth between human populations, and between hominin species, have been attributed to the effect of climatic adaptation. The thermoregulatory principles that form the basis of Allen's (1877) and Bergmann's (1847) rule state that a lower surface-to-volume ratio is adaptive in endotherms living in colder environments, and has been used to explain the increase in pelvic breadth with latitude observed in living humans (Ruff, 1991, 1994, 2002; Weaver, 2002; Holliday and Hilton, 2010; Cowgill et al., 2012), and extinct hominin species (Ruff, 1994, 1995; Holliday, 1997a; Weaver, 2009; Weaver and Hublin, 2009).

An important factor affecting phenotypic variation, however, is missing from these studies. Neutral evolutionary processes (i.e. mutation, drift and migration) are expected to have an influence on phenotypic diversity both at a micro- and a macro-evolutionary level (Roseman and Weaver, 2007; von Cramon-Taubadel and Weaver, 2009). Phylogenetic relationships between closely related species and between populations are often correlated with geographic distance, and can show partial collinearity with climatic differences. For this reason, it is particularly important to take into account the neutral phylogenetic pattern before testing for any effect of climate, so as to avoid the risk of overestimating the effect of climatic selection (Felsenstein, 1985; Martins and Hansen, 1997; Nunn and Barton, 2001). In this respect, it is worth noting that the neutral phylogeographic pattern is the null hypothesis against which any effect of selection should be tested (Roseman and Weaver, 2007).

The results of this study confirm the importance of neutral processes in shaping os coxae variation, in accordance with recent studies that revealed a significant signature of the modern human expansion out of Africa on within-population pelvic shape diversity (Betti et al., 2012; Betti et al., 2013).The most important result of the analyses, in fact, is that pelvic shape differences between human populations show a strong neutral demographic history signature, comparable with that previously found for the cranium (e.g., Relethford, 2004a; Hubbe et al., 2009; Betti et al., 2010; von Cramon-Taubadel, 2014). Indeed, this suggests that a substantial proportion of coxal shape differences between globally distributed populations can be accounted for by neutral processes related to past dispersal events and recurrent gene flow (i.e. population history).

On the other hand, the presence of a signal of neutral population history does not necessarily rule out the possibility of diversifying selection or plasticity playing a role in shaping global patterns of os coxae shape and size variation. Indeed, the analyses confirm a significant (albeit weak) effect of minimum temperature and precipitation on the size and shape of the os coxae even after correcting for neutral processes, partially explaining variation between populations living in different environments (Table 2 and Table 4).

Bergmann's (1847) rule predicts an isometric increase in body size, and by extension coxal size, following the adaptation to colder climates. Our results support this prediction, indicating that populations living in colder environments tend to have absolutely larger pelvic bones than populations from hot climates. An increase in size of the os coxae in high-latitude populations is in agreement with the pattern of increasing pelvic breadth described by other authors and expected under Ruff's cylindrical model (e.g., Ruff, 1991, 1994, 2002; Weaver, 2002; Kurki, 2013). Spatial autocorrelation, or the tendency of geographically closer populations to show a higher degree of similarity because of shared recent ancestry and gene flow, might be expected to have a significant impact on coxal size. However, when the effect of geographic proximity was controlled for, the correlations between coxal size and minimum temperature, and between coxal size and precipitation, were still significant, at least in the male dataset (Table 2).

There are no specific expectations regarding how coxal shape should be affected by climate in the case of adaptation to different climatic conditions. Under the general theoretical framework shared by both Bergmann's (1844) and Allen's (1874) rules, any shape change in the populations that would affect the surface-to-volume ratio of the body could in principle be initiated by climate-driven natural selection. A cold-adapted larger pelvis – in accordance with Ruff's (1991, 1994) cylindrical model – could be achieved by either an isometric increase in the size of the os coxae or by a change in shape that would return a larger breadth of the pelvic girdle at parity of bone size. When shape differences between populations were examined, the results showed a significant correlation with differences in temperature. Even after correcting for the effects of geographic distance (i.e. population history), minimum and maximum temperature significantly contributed to coxal shape differences in males, although minimum temperature did not reach significance in females (Table 4). However, the effect of temperature appears reduced once neutral processes are accounted for, revealing a tendency to overestimate the signal when population history is not explicitly included in the model. von Cramon-Taubadel (2009) and Betti et al. (2010) found a similar decrease in the correlation of climate with cranial variation once the neutral pattern was taken into account. The overestimation of the effect of selection appears to be a recurrent risk in studies of human phenotypic variation, confirming the importance of explicitly modeling the underlying neutral variation structure together with the hypothetical selective factors.

When the changes in shape along the PLS axes were analyzed, differences in morphology significantly associated with climate were very similar in males and females, but too subtle and diffused to be readily described and interpreted. It is also worth noting that in both sexes the overall correlation between shape and climate, as captured by the PLS axes, is relatively small (RV coefficient < 0.09). In addition, it is not straightforward to relate the small morphological differences reflected by these shape components with their effect on the articulated pelvic girdle. It is, therefore, difficult to directly compare these results with the expectations of Ruff's (1991, 1994) cylindrical model, which predicts larger bi-iliac breadth in high-latitude populations. On the other hand, the results of this study support a correlation between both size and shape of the os coxae and climate, which are compatible with Ruff's (1991, 1994) model, and follow the expectations of Bergmann's (1844) rule.

The differences between the sexes, especially in the strength of the correlation with the climatic variables, could be a consequence of a higher level of evolutionary constraints in the female pelvis, due to obstetrical requirements. The fact that the male sample is larger does not appear to be a sufficient explanation for the stronger effects of climate on coxal shape in respect to the female sample. In fact, male shape variation still shows a higher correlation with climate even when the dataset is reduced to the same number of populations and individuals in both sexes.

The overall picture that emerges from the analyses is similar to that described for cranial variation, where both neutral and selective processes contribute to explain population differences in morphology (Roseman and Weaver, 2004; Harvati and Weaver, 2006; Smith, 2009; von Cramon-Taubadel, 2009, 2014; Betti et al., 2010). The two processes are compatible and not mutually exclusive, although neutral processes appear to have left a much stronger signature on global patterns of population diversity than climatic adaptation. Importantly, the results underline the risk of overestimating the effect of selection (in this case related to climate) if the underlying neutral pattern due to population history is not taken into consideration.

Beyond their direct relevance to understanding modern human microevolutionary history, the results have important implications for the interpretation of pelvic differences between hominin species. Differences in cranial shape between modern humans and Neanderthals, in some cases interpreted in the light of climatic adaptation (Coon, 1962; Beals et al., 1983; Franciscus, 2003; Holton and Franciscus, 2008) have been recently shown to be compatible with neutral phenotypic evolution in the two lineages (Roseman and Weaver, 2007; Weaver et al., 2007, 2008). These recent studies highlighted the importance of neutral processes in generating morphological differences not only within our species, but also between closely-related species. In a similar way, differences in pelvic shape between Neanderthals and modern humans have been attributed to the adaptation of the former to colder climates (Ruff, 1994, 1995; Holliday, 1997a; Weaver, 2009; Weaver and Hublin, 2009). In the light of these new results, suggesting a substantial effect of neutral evolutionary processes on the human pelvis, and a limited effect of climatic selection, it may be necessary to re-evaluate previous adaptive interpretations of hominin pelvic shape differences.

In conclusion, the results of this study reveal a very strong signature of population history in shaping pelvic bone variation within our species. At the same time, climatic adaptation had a significant, albeit more limited effect, contributing to the variation in pelvic morphology observed in human populations inhabiting different latitudes. The effect of climate appears markedly decreased when the signature of neutral evolutionary processes is explicitly accounted for, highlighting the importance of including neutral processes when testing for the effect of selective factors on pelvic morphology within or between hominin species.

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Table 1: Population samples and institutions where the material is curated.

Region	Males	Females	Institution[a]
Africa			
Botswana, Tswana	33	30	UW
Egypt dynastic	34	17	AMNH, NM
Kenya, Kykuyu	40	30	NMK
Lesotho, Sotho		34	UW
Malawi	33		UW
Nubia	33	25	NM
South Africa, Khoi-San	26	21	AMNH, MGM, NHM, UW
South Africa, Venda	29		UW
Swaziland	39	20	UW
Europe			
Austria	70	16	CMNH, NM
France	28	23	MdH
Ireland	28		CMNH
Italy	33	12	CMNH, MNdAE
Portugal	42	42	CU
Western Russia	26		CMNH
Asia			
Ainu, Japan	23	20	KU, TU
Andaman Islands	11		MdH, DC
India	28		AMNH, MdH, MoM, NHM, UW

Iran	32	22	UP
Japan	45	37	AMNH, KU, MdH, NH
Philippines, ‘negritos’	8	8	MdH
Thailand	37	36	CMU, MdH
America			
Alaska, Point Hope	38	35	AMNH
Argentina, Patagonia	33	13	MdH, MNdAE
Canada, Sadiermiut	24	24	MCC
Chile, Fuegians	17	10	MNdAE, NHM, UR
Native Californians	36	31	UCB
Peru	31	33	MdH, UCB
South Dakota, Arikara	35	33	UTK
Tennessee, Late Mississippian	18		UTK
Oceania			
Australia	12		AMNH, MdH, MNdAE, DC

[a]*(AMNH = American Museum of Natural History, New York, USA; CMNH = Cleveland Museum of Natural History, Ohio, USA; CMU = Chiang Mai University, Thailand; CU = Coimbra University, Portugal; DC = Duckworth Collection, University of Cambridge, UK; KU = Kyoto University, Japan; MCC = Musée Canadien des Civilisations, Gatineau, Canada; MdH = Musée de l’Homme, Paris, France; MNdAE = Museo Nazionale di Antropologia e Etnologia, Firenze, Italy; NHM = Natural History Museum, London, UK; NM = Naturhistorisches Museum, Wien, Austria; NMK = National Museum of Kenya, Nairobi, Kenya; TU = Tokyo University, Japan; UTK = University of Tennessee at Knoxville, USA; MoM = San Diego Museum of Man, California, USA; MGM = McGregor Museum, Kimberley, South Africa; UCB = University of California*

at Berkeley, USA; UP = University of Pennsylvania at Philadelphia, USA; UR = University of Rome "La Sapienza", Italy; UW = University of Witwatersrand, Johannesburg, South Africa).

Table 2: Results of the correlation between average population coxal size and each climatic variable. R^2 and p-value are estimated after a simple linear regression analysis. Significant results in bold.

Model[a] (males)	**R^2**	**P-value**	**P-value ANOVA[b]**	**New p-value[c]**
size VS Tmin	0.426	< 0.001	**0.034** CorSpher	**0.006**
size VS Tmax	0.219	0.009	**0.007** CorRatio	0.614
size VS Prec	0.252	0.005	**< 0.001** CorRatio	**< 0.001**
Model (females)	**R^2**	**P-value**	**P-value ANOVA**	**New p-value**
size VS Tmin	0.323	0.005	**0.027** CorRatio	0.111
size VS Tmax	0.129	0.093	**0.006** CorRatio	0.971
size VS Prec	0.102	0.138	**0.002** CorRatio	0.250

[a] Tmin = Minimum Temperature, Tmax = Maximum Temperature, Prec = Precipitation.

[b] Results of ANOVA test comparing the simpler linear model with the generalized least square model that accounted for spatial autocorrelation (p-value ANOVA). A significant result ($\alpha \leq 0.05$) implies that spatial autocorrelation is a significant factor in the model. The type of spatial autocorrelation is specified in the table (CorSpher = spheric, CorRatio = rational quadratic).

[c] New p-value obtained including spatial autocorrelation in the model.

Table 3: Results of the correlation between average population coxal size and each of the climatic variables in 22 populations that included both male and female individuals. R^2 and p-value are estimated after a simple linear regression analysis. Significant results in bold.

Model[a] (males)	R^2	P-value	P-value ANOVA[b]	New p-value[c]
size VS Tmin	0.310	**0.005**	n.s.	
size VS Tmax	0.135	0.089	**0.036** CorRatio	0.712
size VS Prec	0.104	0.142	**0.013** CorRatio	0.235
Model (females)	R^2	**P-value**	**P-value ANOVA**	**New p-value**
size VS Tmin	0.343	0.004	**0.042** CorRatio	0.221
size VS Tmax	0.156	0.069	**0.005** CorRatio	0.500
size VS Prec	0.126	0.105	**0.002** CorRatio	0.246

[a] Tmin = Minimum Temperature, Tmax = Maximum Temperature, Prec = Precipitation.

[b] Results of ANOVA test comparing the simpler linear model with the generalized least square model that accounted for spatial autocorrelation (p-value ANOVA). A significant result ($\alpha \leq 0.05$) implies that spatial autocorrelation is a significant factor in the model. The type of spatial autocorrelation is specified in the table (CorRatio = rational quadratic).

[c] New p-value obtained including spatial autocorrelation in the model.

Table 4: Results of the Mantel tests between population coxal shape differences (Q) and climatic distances. The values obtained after correcting for the non-linear model of the demographic history signature are also reported. Significant results in bold.

Model[a] (males)	R^2	P-value	Model (females)	R^2	P-value
Q VS Tmin.d	0.185	**< 0.001**	Q VS Tmin.d	0.049	**0.021**
Q VS Tmax.d	0.089	**< 0.001**	Q VS Tmax.d	0.054	**0.006**
Q VS Prec.d	0.022	0.084	Q VS Prec.d	0.002	0.337

Q VS Tmin.d / DHS	0.108	**< 0.001**	Q VS Tmin.d / DHS	0.041	0.262
Q VS Tmax.d / DHS	0.053	**0.005**	Q VS Tmax.d / DHS	0.055	**0.031**
Q VS Prec.d / DHS	0.024	0.310	Q VS Prec.d / DHS	0.034	0.599

[a] Q: matrix of shape differences**;** Tmin.d, Tmax.d and Prec.d: distance matrices based on minimum temperature, maximum temperature and precipitation; DHS: demographic history signature.

Table 5: Results of the Mantel tests between population coxal shape differences (Q) and climatic distances on the 22 populations for which both sexes were available. The values obtained after correcting for the non-linear model of the demographic history signature are also reported. Significant results in bold

Model[a] (males)	**R^2**	**P-value**	**Model (females)**	**R^2**	**P-value**
Q VS Tmin.d	0.183	**< 0.001**	Q VS Tmin.d	0.048	**0.033**
Q VS Tmax.d	0.070	**0.006**	Q VS Tmax.d	0.053	**0.011**
Q VS Prec.d	0.050	**0.031**	Q VS Prec.d	0.001	0.391
Q VS Tmin.d / DHS	0.129	**< 0.001**	Q VS Tmin.d / DHS	0.053	0.298
Q VS Tmax.d / DHS	0.084	**0.013**	Q VS Tmax.d / DHS	0.065	0.061
Q VS Prec.d / DHS	0.060	0.163	Q VS Prec.d / DHS	0.045	0.625

[a] Q: matrix of shape differences**;** Tmin.d, Tmax.d and Prec.d: distance matrices based on minimum temperature, maximum temperature and precipitation; DHS: demographic history signature.

Table 6: PLS coefficients for the three climatic variables.

	MALES	**FEMALES**

	PLS 1	**PLS 2**	**PLS 1**	**PLS 2**
Tmin[a]	0.764	0.134	0.740	0.010
Tmax	0.642	-0.254	0.659	0.187
Prec	0.063	0.958	0.133	-0.982

[a] Tmin = Minimum Temperature, Tmax = Maximum Temperature, Prec = Precipitation.

Figures

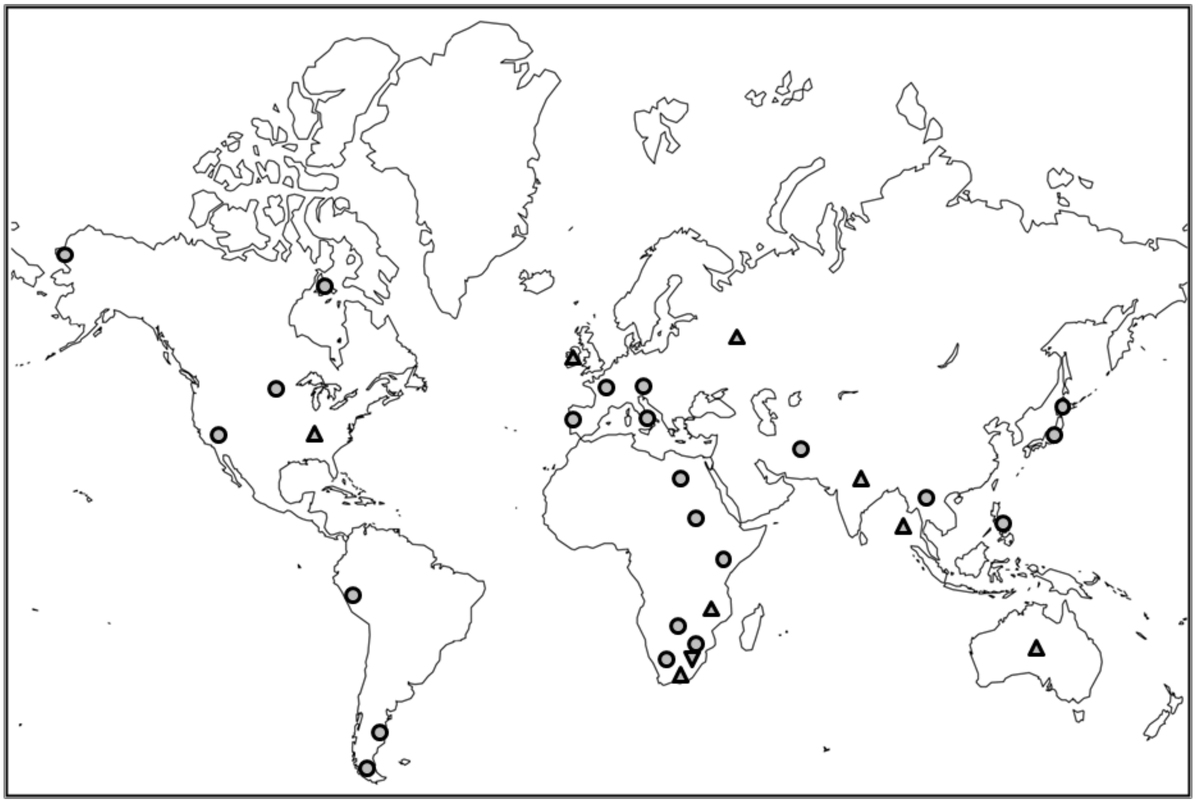


Figure 1: **Geographic location of population samples used in this study.** Circles = population samples including both sexes; upward-pointing triangles =males only; downward-pointing triangles = females only.

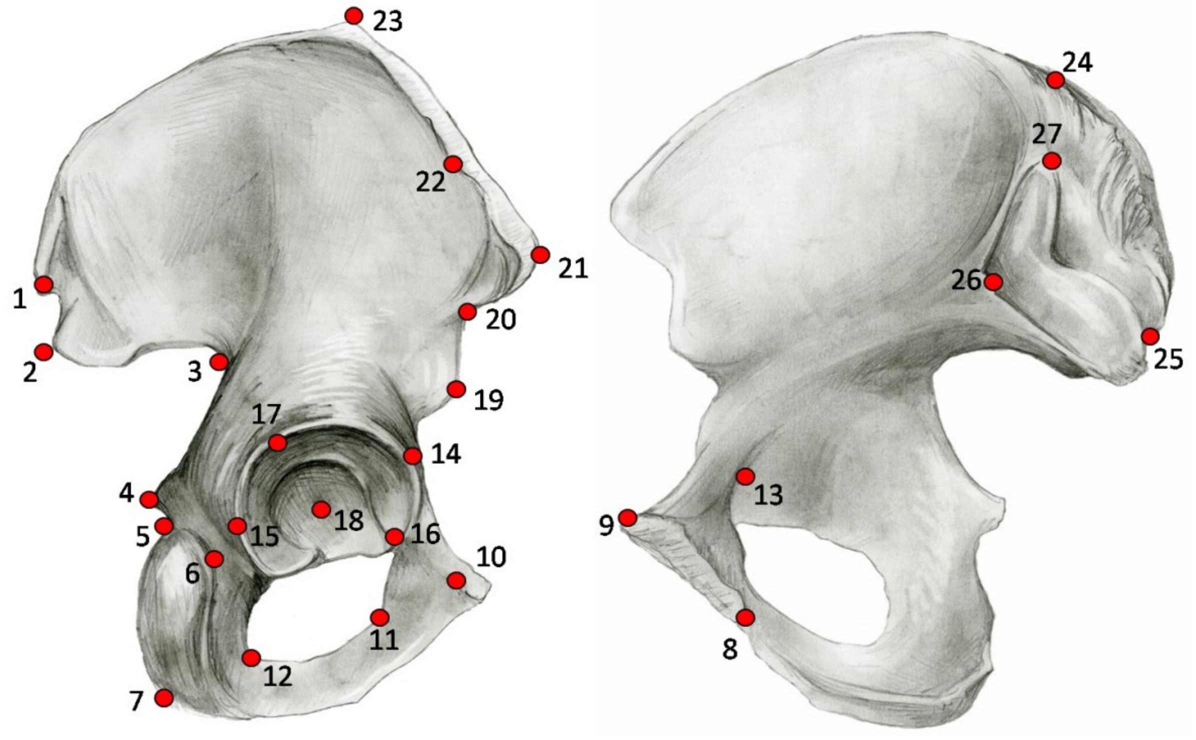


Figure 2: **Landmarks of the os coxae used in this study**. The right os coxae is depicted from a lateral view on the left, and from a medial view on the right.

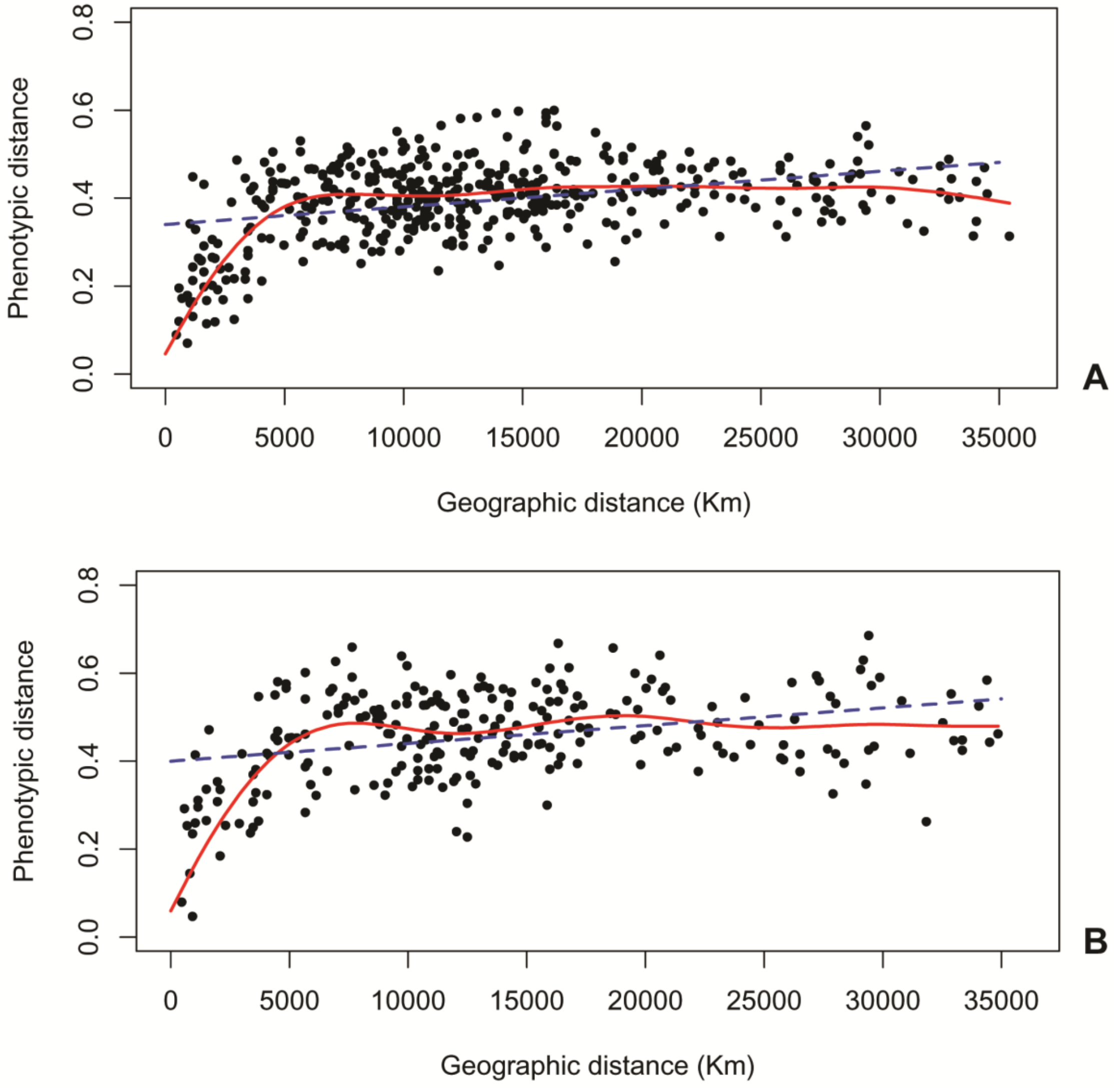
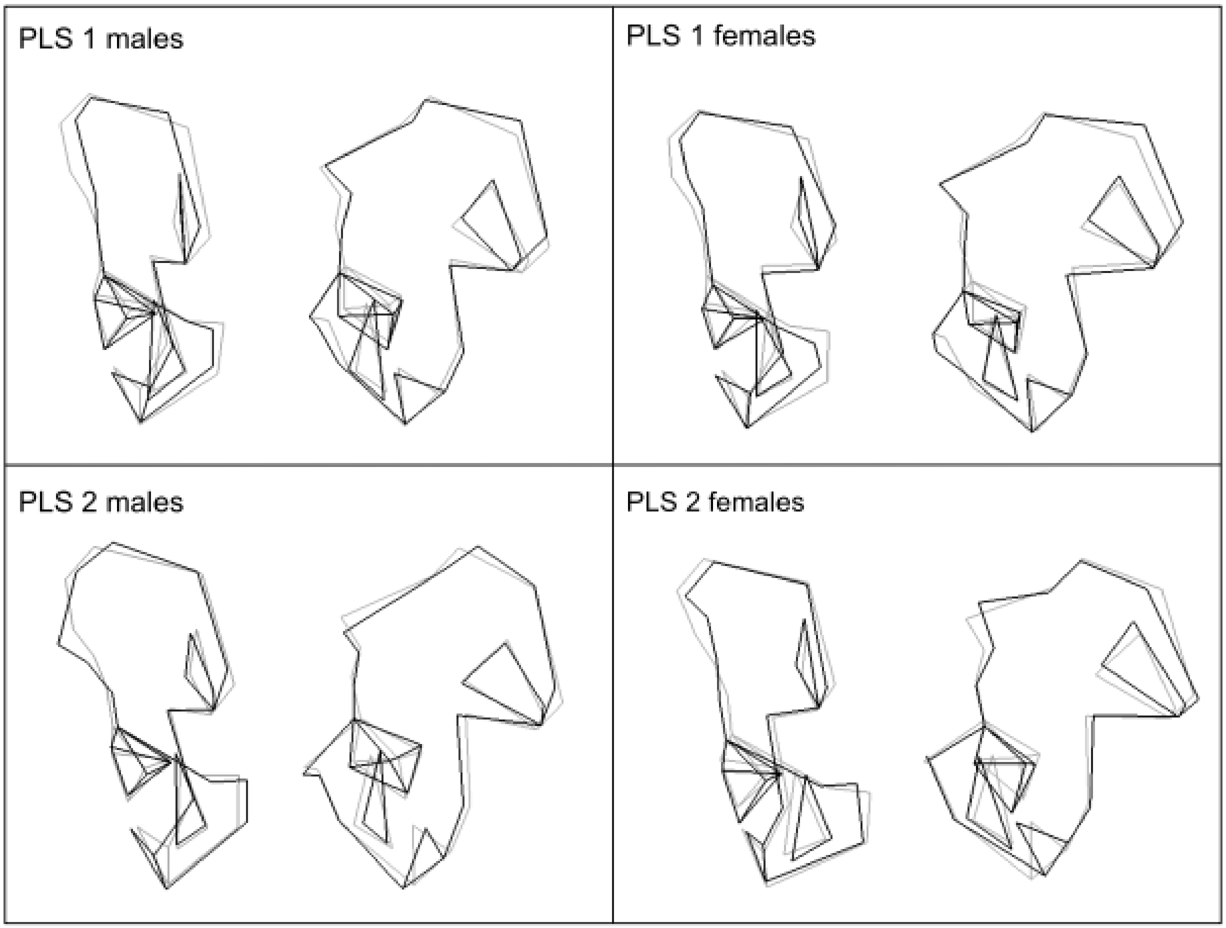


Figure 3: Plots of between-population phenotypic distance and geographic distance for males (A) and females (B). Each circle represents a pair of populations. The fit with a linear and a non-linear model of the neutral signature of past population history are represented by a dashed blue line and a full red line, respectively.

Figure 4: **Shape changes along PLS 1 and PLS 2 axes**. The two landmark configurations (frontal and medial views) represent the lowest and highest PLS scores (in grey and black, respectively). Please note that for PLS 2, the relationship with climate is reversed in females with respect to males (see Table 6).



SUPPLEMENTARY MATERIAL

Table S1: Subsets of the dataset used to test the accuracy of visual sex determination. The sex discriminant function obtained from DB1 was applied to DB2 and DB3. The proportion of individuals whose sex matched the results of the discriminant function is calculated. DB1: individuals of known sex used to derive the discriminant function; DB2: separate dataset of known-sex individuals on whom the discriminant function was applied; DB3: estimated-sex individuals on whom the discriminant function was applied.

Population samples	**Males**	**Females**	**Total**	**Proportion of individuals of matching sex (%)**
DB1	169	165	334	
Africa	*62*	*64*		
Europe	*70*	*65*		
Asia	*37*	*36*		
DB2	253	71	324	98.8
Africa	*79*	*21*		
Europe	*157*	*22*		
Asia	*17*	*28*		
DB3	500	336	836	98.2

Africa	*126*	*92*
Europe		*6*
Asia	*130*	*59*
Americas	*232*	*179*
Australia	*12*	

Table S2: Climatic data for the population samples.

Region	Minimum Temperature (°C)	Maximum Temperature (°C)	Precipitation (mm)
Ainu, Japan	-16.5	20.7	1547
Alaska, Point Hope	-26.7	10.3	238
Andaman Islands	22.3	31.5	3069
Argentina, Patagonia	-15	32.4	469
Australia	4.3	37	203
Austria	-10.1	17	1361
Botswana, Tswana	5	33.2	362
Canada, Sadiermiut	3.1	30	496
Chile, Fuegians	6.9	34.9	17
Egypt dynastic	0.8	24.8	635
France	-2.6	12.2	812
India	12.6	35.9	1663

Iran	-5	36	170
Ireland	1.6	18.8	984
Italy	3.8	30	771
Japan	-7.9	28.1	1201
Kenya, Kykuyu	15.6	33.9	461
Lesotho, Sotho	-2.7	23.7	675
Malawi	1.5	34.9	261
Native Californians	-3.8	32.2	1221
Nubia	14.7	32.2	1147
Peru	14	38.7	386
Philippines, ‘negritos’	-6.2	22.6	187
Portugal	-1.5	18.4	855
South Africa, Khoi-San	22.6	32.6	2214
South Africa, Venda	5.1	28.1	1018
South Dakota, Arikara	-12.3	23.1	678
Swaziland	-34.5	13.8	264
Tennessee, Late Mississippian	8.1	29.3	724
Thailand	12.8	36	1181
Western Russia	9.8	32.5	387

Table S3: Results of the partial Mantel tests between population pelvic shape differences (Q) and climatic distances (Tmin.d, Tmax.d and Prec.d, respectively distance matrices based on minimum temperature, maximum temperature and precipitation), correcting for geographic distance (D). Significant results in bold.

Model (males)	**R^2**	**P-value**	**Model (females)**	**R^2**	**P-value**
Q VS Tmin.d / D	0.150	**<0.001**	Q VS Tmin.d / D	0.048	**0.025**
Q VS Tmax.d / D	0.037	**0.027**	Q VS Tmax.d / D	0.029	**0.035**
Q VS Prec.d / D	0.042	0.056	Q VS Prec.d / D	0.002	0.372

Table S4: Correlation between block 1 (shape variables) and block 2 (climatic variables) for the three PLS axes.

	MALES		**FEMALES**	
	Correlation	**P-value**	**Correlation**	**P-value**
PLS 1	0.483	< 0.001	0.522	< 0.001
PLS 2	0.373	< 0.001	0.448	< 0.001
PLS 3	0.266	< 0.001	0.327	< 0.001