The relative role of drift and selection in shaping the human skull

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Abstract

Human populations across the world vary greatly in cranial morphology. It is highly debated to what extent this variability has accumulated through neutral processes (genetic drift) or through natural selection driven by climate. By taking advantage of recent work showing that geographic distance along landmasses is an excellent proxy for neutral genetic differentiation, we quantify the relative role of drift versus selection in an exceptionally large dataset of human skulls. We show that neutral processes have been much more important than climate in shaping the human cranium. We further demonstrate that a large proportion of the signal for natural selection comes from populations from extremely cold regions. More generally, we show that, if drift is not explicitly accounted for, the effect of natural selection can be greatly overestimated.

The extent to which climate has shaped the cranium is still highly debated. While some authors have reported a significant effect of natural selection on some cranial traits (e.g. Beals et al. 1984; Harvati and Weaver 2006; Roseman 2004), other studies have failed to find any sizable link between climate and cranial morphology (Betti et al. 2009; Manica et al. 2007; Relethford 2004a; Roseman and Weaver 2007; von Cramon-Taubadel and Lycett 2008). An important difference among these studies is that they deal with different phenotypic metrics that refer either to the size, the shape or the form (size and shape) of the cranium. In general, studies that have looked at size related metrics (either size or form), have detected signatures of selection by climate. For example, the size and breadth of the nasal aperture are often considered under selective pressures related to thermoregulatory breathing strategies (Carey and Steegmann 1981; Franciscus and Long 1991), and a rounded, brachicephalic cranium has been suggested to be an adaptation to cold climate, thanks to the reduced surface:mass ratio (Beals et al. 1984). On the other hand, studies focusing on shape have found very limited links of climate. For example, the shape of the temporal bone has been argued to reflect mostly ancient demography (Smith HF et al. 2007), and similar results have been recently obtained for several other cranial bones, such as the sphenoid, frontal and temporal bone (von Cramon-Taubadel in press). Even in cases where shape has been linked to climate, such as for the shape of the maxilla bone (von Cramon-Taubadel in press), this effect is of limited magnitude.

A major complication in assessing the effect of climate on craniometric traits, irrespective of the phenotypic metric used, arises from the fact that populations affected by similar climatic conditions are often geographically close to each other. Thus, even when we find shared craniometric characteristics among populations from similar climates, we should not jump to the conclusion that these imply natural selection. Such similarity could simply reflect the recent common ancestry and/or recent genetic exchange due to their proximity.

A central tenet of population genetics is that, when looking for selection in the spatial distribution of allele frequencies, we have first to account for patterns that can be explained by neutral processes (i.e. drift) (Smouse et al. 1986; Sokal et al. 2000). Roseman (2004), and von-Cramon-Taubadel (in press) approached this problem by using populations for which both genetic and phenotypic data were available, using the neutral genetic information to control for the effect of past demography when investigating selection on cranial traits. Harvati and Weaver (2006) also used neutral genetic information, but only compared the fit between phenotypic distance and genetic distances versus the fit with climatic distances rather than explicitly correcting for past demography. A drawback of this approach is that these studies were limited to a very small number of populations (n=10, 12 and 13 respectively). Recent work on global genetic datasets has demonstrated a very strong correlation (R~0.9) between genetic distance and geographic distance measured along landmasses to mimic human migrations (Manica et al. 2005; Ramachandran et al. 2005; Romero et al. 2008). Such a perfect match implies that, in large scale analyses, geography can be used as an adequate proxy for ancient demography (Lawson Handley et al. 2007). This important finding allows us to investigate the role of drift and selection in large phenotypic datasets without matching genetic datasets. To our knowledge, this approach has only been adopted once by Relethford (2004a), who looked at full and partial Mantel correlations between phenotypic distance, geographic distance and average temperature for 26 populations measured by Howells.

In this paper, we investigated the role of climate in explaining differentiation among human populations by analyzing a large global dataset of craniometric traits (Hanihara and Ishida 2001; 2005; Manica et al. 2007). We used phenotypic measures that mostly characterize the size and form of the cranium, rather than the shape of individual bones, as the former have been argued in the past to be the most affected by climate. We first test to what extent phenotypic differentiation can be explained by geographic proximity (a proxy for neutral genetic differentiation), by looking at the relationship between pairwise phenotypic distances among populations and pairwise geographic distances (using both a linear Isolation By Distance model and a more realistic non-linear IBD model). We then test for climatic effects that are above and beyond the patterns due to geographic proximity by correlating pairwise phenotypic distances with pairwise differences in three climatic variables (minimum and maximum temperature, and precipitation) after correcting for IBD.

MATERIALS AND METHODS

Datasets and distance matrices

We used a large worldwide dataset of 37 morphometric measurements (for a detailed description of the traits see Table S1) from 4,666 male individuals belonging to 105 populations and 1,579 females drawn from 39 populations (Fig. 1; for a detailed list see Table S2) (Hanihara and Ishida 2001; 2005; Manica et al. 2007). To reduce the possible sampling bias, a minimum sample size of 15 individuals per population was enforced (median size = 36), and only samples younger than 2,000 years were included in the analyses. The raw data were transformed into Z-scores to allow the direct comparison of different cranial traits. Beside analyzing the two sexes separately, we also repeated all our analyses excluding the Inuits, Eskimos and other populations living in regions with minimum annual temperature lower than -20°C, to verify the effect of extreme climatic conditions.

A matrix of phenotypic distances between populations, based on morphometric traits, was computed following Relethford and Blangero (1990) and Relethford and colleagues (1997). The method treats morphometric data as genetic markers, and derives a matrix of genetic distances (***Q***) from the pooled within-population phenotypic covariance matrices scaled on the traits' heritability (h^2). Because an estimate of heritability is at present available for only a few traits in specific populations (Arya et al. 2002; Carson 2006), we applied a conservative approach and we scaled the covariance matrix to h^2=1. Scaling the matrix to h^2=1 assumes that the phenotypic covariance matrix is proportional to the additive genetic covariance matrix, an assumption that is supported by previous studies (e.g. Cheverud 1988; Gonzalez-Jose et al. 2004). It is possible to scale the phenotypic covariance matrix to an estimated average heritability for cranial traits (h^2=0.55 or h^2=0.36, Relethford 1994; Weaver et al. 2008), but the result would be a matrix of genetic distance proportional to the previous one, with no effect on the relative genetic distance of populations (Relethford 2004a).

The default approach is to assume identical population size in every population. An alternative is to take advantage of the linear relationship between distance from Sub-Saharan Africa and within-population mean coalescence time (Liu et al. 2006), which equals twice the effective population size (Balloux et al. 2003; Laporte and Charlesworth 2002). We estimated mean coalescence time, and thus effective sizes, for all populations from our dataset based on their distance from Sub-Saharan Africa, and used these estimates to compute **Q**. Since the results were not affected by whether **Q** was corrected or not for population size, we only present results from the corrected estimates in this paper. We also corrected the phenotypic covariance matrices for the sample size, as suggested by Relethford and colleagues (1997). Since **Q** distances between populations are effectively ratios, we normalized the matrix using an arcsine square root transformation. All computations were performed in R version 2.6.1 (R Development Core Team 2007), and the results were validated using Relethford's software RMET version 5.0 (available at http://konig.la.utk.edu/relethsoft.html) on a smaller dataset (our dataset was too large for RMET).

A matrix of pairwise geographic distances (***D***) was computed between populations. The distance between populations was calculated as the shortest route on landmasses, avoiding areas with a mean altitude higher than 2,000 meters over sea level (Manica et al. 2005; Prugnolle et al. 2005). Connections between Africa and Eurasia were through the Sinai Peninsula (no direct exit through the Horn of Africa was allowed), and movement between Eurasia and America through an assumed land bridge on the Bering Strait. Land bridges were also assumed between the Malay Peninsula and Australia, connecting the major Indonesian islands. Three different climatic distance matrices [minimum annual temperature (***Tmin***), maximum annual temperature (***Tmax***) and mean annual precipitation (***P***)] were computed as pairwise Euclidean distances from WORLDCLIM, a set of global climatic GIS layers interpolating data from approximately 15,000 weather stations distributed worldwide (Hijmans et al. 2005).

Statistical analysis

We first tested the relationship between phenotypic and geographic distances (**Q** vs **D).** Beside modeling Isolation By Distance (IBD) as a linear relationship (tested with a Mantel test with 10,000 randomizations), we also fitted a non-linear model based on Malecot’s coefficient of kinship (Morton 1973; Morton 1975; Morton et al. 1971; Relethford 1980; Relethford and Lees 1982; Zegura et al. 1995):

$$q_{ij}^2 = A' \left(1 - e^{-bd}\right)$$

where q_{ij} is the phenotypic distance between populations *i* and *j*, *A*' is the value to which the phenotypic distance tends asymptotically to when geographic distance (d_{ij}) increases, and *b* is the rate of increase in phenotypic distance. We first found parameters values by non-linear least square optimization, and then tested the significance of the fit (measured in terms of proportion of explained variance, R^2) through a randomization approach analogous to the one used for the Mantel tests. As the non-linear IBD model explained sizably more variance than the linear version (32.1% vs. 19.9% for males, Table 1), all later analyses were based on the non-linear model.

The relationship between phenotypic distance and the three climatic variables was first estimated directly (i.e. without correcting for geography) with a series of Mantel tests. We then fitted partial Mantel correlations between phenotypic distance and climatic variables after accounting for geography, which acted as a proxy for ancient demography. Thus we first fitted the non-linear IBD relationship and then tested for a linear association with the climatic variables. Significance was assessed by randomizations (n=10,000). Tests were one-tailed to maximize the power of detecting positive relationships, which are biologically meaningful. The fit was expressed as percentage of explained variance (R^2), an intuitive measure with an easy to interpret biological meaning, and arguable the most appropriate measure to compare linear and non-linear models. For comparison with previous analyses by other authors, we also provide partial correlation coefficients in supplementary tables (the two measures can not be easily converted to each other).

The same approach was repeated for individual morphometric traits, in order to test for different responses depending on the cranial features considered. As measurement error is more likely to affect smaller traits, we tested whether our ability to detect a link between climate and individual traits was affected by the size the traits. We tested for such an effect by plotting the magnitude of the trait specific correlation coefficients against the mean size of the traits. We found no relationship between trait size and the strength of the relationship between phenotypic differentiation and geographic distance or climate (Figure S1).

RESULTS

Under a linear IBD model, geographic distance between pairs of populations is a good predictor of phenotypic differentiation in males as well as in females (R^2=21% and 25% respectively, Table 1; equivalent conclusions can be drawn using partial correlations, Table S3). A non-linear IBD model does even better, with distance explaining 33% for both males and females (Table 1 & S3; Fig. 2 A&B). Beside explaining the same amount of variance, the parameter values for the IBD models are almost identical in the two sexes (for males: $A'=0.561\pm0.003$, $b=0.00030\pm0.00001$; for females: $A'=0.575\pm0.006$, $b=0.00039\pm0.00002$). This relationship is robust to the removal of populations from extreme climates (the Inuits, Eskimos and other populations living in regions with minimum annual temperature lower than -20°C; Table 1). The relationship remains strong and significant even if we first corrected for climatic variables ($R^2\geq26.5\%$, $p<0.001$ for males, and $R^2\geq27.0\%$, $p<0.001$ for females).

Minimum and maximum temperature (but not precipitation) are also significant predictors of phenotypic differentiation between populations, but their explanatory power (R^2 ranging from 11% to 18%) is much lower than geography, and is largely driven by populations from extremely cold climates (Table 1). With the exception of maximum temperature in females, excluding such populations leads to a sizable reduction in R^2 (Table 1). The relationship with climate becomes even weaker if we account for isolation by distance (Table 1). As geographic distance and climatic differences are collinear, not accounting for isolation by distance leads to overestimating the effect of climate on phenotypic differentiation among populations.

The relative effect of climate and geographic distance in determining phenotypic differentiation differs greatly for individual cranial traits (Table 2 & S4). Most of the traits show a significant correlation with minimum and/or maximum temperature, while only two of them are significantly but very weakly associated to annual precipitation. The correlation with climate always decreases after correcting for the IBD pattern. The traits showing a stronger correlation with climate are mainly related to facial breadth (e.g. M11, AUB), or to the dimensions of the orbits and nasal aperture (e.g. OBH, NLA, NPH).

DISCUSSION

Isolation By Distance proved a very good predictor of between-populations phenotypic differentiation, confirming Relethford's findings on a smaller dataset (2004b). Interestingly, the slope we estimated for the non-linear IBD function is almost identical to the value obtained by Relethford (2004b) on a different dataset, suggesting that our reconstruction of neutral differentiation is robust and not dependent on the populations used in the analysis. Minimum and maximum temperature, when considered in isolation, showed a moderate link with phenotypic differentiation. Climatic variables had much weaker explanatory power than geographic distance and, more importantly, their role was much reduced once we accounted for the underlaying isolation by distance pattern. This important result illustrates that, since populations that are close by also tend to experience similar climatic conditions, it is essential to account explicitly for isolation by distance to avoid overestimating the effect of climate.

It is intriguing that both Roseman (2004) and Relethford (2004a), on the contrary, found an increase in correlation with climate after accounting for the neutral genetic pattern, even though both these studies use the same measurements considered in our work. Both works are also directly comparable with the present one, as they do not use size-corrected data, analyzing form and not shape. However, their studies were characterized by rather small sample sizes (10 and 26 populations, respectively) compared to our study (105 populations for male and 39 for females). Also, there might be limitations in the way neutral genetic patterns were modeled in these two studies. In the case of Roseman (2004), perfectly matched samples for the genetic and morphometric traits were not available, and genetic data from neighboring populations had to be used instead. Relethford (2004a) used geography as proxy for neutral genetics as we did in our analysis, but only modeled isolation by distance as a linear function. In our dataset, a non-linear saturating function did much better, and this also applies to the dataset used by Relethford [as proven by Relethford himself (2004b) in another analysis of that dataset]. Until appropriate datasets containing matching genotypic and phenotypic measurements become available, extracting the neutral information (i.e. drift) from the traits themselves (as illustrated in this paper) is a viable and desirable option, preferably using more realistic, non-linear IBD functions.

It is interesting that excluding populations from extremely cold regions erases the correlation with minimum temperature and reduces the correlation with maximum temperature. Our results confirm Roseman's (2004) observation that his one population from cold regions seemed to differ significantly from the other nine populations from temperate and tropical climates. Why should populations from extreme cold regions differ so strongly from the rest of the world? One possibility is that temperatures below a certain threshold lead to a plastic response in cranial development, but previous work has shown very limited influence of climate on most measurements during the growth and development of the cranium (Relethford 2004a; Sparks and Jantz 2002). Another possibility is that our climatic variables are somewhat crude, and thus only allow us to pick up a link with climate only for extreme temperatures, when the magnitude of the effect is large enough to be distinguished from the noise. Alternatively, it is possible that behavioural adaptation, possibly through cultural evolution, is effective in buffering the effect of cold climate up to a certain threshold, beyond which selective pressure becomes strong enough to cause the climate related changes in phenotype detected by our study as well as several others (e.g. Beals et al. 1984; Harvati and Weaver 2006; Roseman 2004).

The fact that we detected a role for climate in driving between-population differentiation is not at odds with our recent finding on the same dataset that climate does not affect within-population phenotypic diversity (Betti et al. in press). Between-population differentiation and within-population diversity can be affected in different ways, depending on the nature of the selective forces. For example, unless directional selection is exceptionally strong, it could shift a trait's mean value without affecting within-population variability. This would translate in an effect of climate on between-population differentiation without leaving any signature on global patterns of within-population phenotypic diversity.

Looking at single traits, the highest correlations with climate are observed for measurements of cranial and facial breadth, and measurements describing the nasal and orbital apertures. It has been suggested that the nasal index responds to selective pressures related to thermoregulatory breathing strategies (Carey and Steegmann 1981; Franciscus and Long

1991). A thermoregulatory hypothesis has also been proposed to explain the pattern of brachycephalization in different populations, and the breadth of the cranium has been shown to highly contribute to the degree of brachycephalization of the cranium (Beals et al. 1984).

It is worth stressing again that considering the whole set of traits and excluding populations living in extremely cold areas eliminates the correlation with minimum temperature and strongly reduces the correlation with maximum temperature. Thus, for populations that do not come from extremely cold climates, cranial measurements can be considered as good neutral markers. The excavation of archeological sites, and specifically burial sites, has provided plenty of specimens now stored in many museums and university collections. These specimens cover in space and time most of human history and prehistory. Despite the recent improvements in the extraction and sequencing of ancient DNA, we are still far from having a transversal view of human genetic variability over the millennia similar to the one available for skeletal remains. Given our results, skeletal morphology can still play a key role in studies of evolution of populations over time, adaptation to local climate, or for reconstructing the affinities of extinct populations with coeval or modern ones.

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Figure Legends

Figure 1: Locations of populations for which skulls from male (black cirlces), female (white circles) and both sexes (grey circles) were available, plotted on global maps of A) maximum temperature, B) minimum temperature and C) precipitation.

Figure 2: Plots of between-population phenotypic distance and geographic distance for A) males and B) females. The fit with a linear regression model and an isolation-by-distance model are represented by a full blue line and a dashed red line, respectively.