Does biological diversity indicate modern human expansion across Africa?

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Abstract

Regardless of whether modern humans originated in a single region of Africa, or across the continent, we may have experienced a significant expansion which crossed Africa before we expanded out of the continent. There are conflicting findings regarding whether we expanded across Africa, and we are known to lack clarity on where the expansion began. The present study explored the expansion by examining types of diversity in sub-Saharan Africans: cranial shape (13 populations), autosomal (20 populations), X-chromosomal (17 populations), and, adjusting for minimum temperature, mitochondrial (20 populations). A ranking procedure indicated, across diversities, where the expansion originated. Each diversity declined with increasing distance from some location in Africa. Findings with autosomal diversity appeared to be driven by the datapoint for Somalis. A southern origin was specified by cranial and X-chromosomal diversities. No singular region was identified by autosomal or mitochondrial diversities. Simultaneous examination of diversities suggested a southern origin. Therefore, within Africa, diversities indicate an expansion from southern Africa. Admixture is a known obstacle for studying expansion. It is explained why results might not have arisen from a broad effect of admixture given that linkage disequilibrium previously pointed to the south.

Introduction

Modern humans originated in Africa (e.g., Cabrera, 2022; Henn et al., 2018), either in one region or across regions (e.g., Henn et al., 2012, 2018; Hublin et al., 2017; Nielsen et al., 2017; Padilla-Iglesias et al., 2025; Scerri et al., 2019). Later, we dispersed out of the continent, populating Eurasia, the Americas, and Oceania (Henn et al., 2012). *Between* our origination and our global dispersal, there may have been an expansion across Africa (the *across-Africa expansion*) (Bergström et al., 2021; Rito et al., 2019) from a single region 60–100 thousand years ago (Henn et al., 2011). The nature of this expansion has been considered, e.g., if it spread to geographical areas which were i) unpopulated by modern humans, or ii) already inhabited by close-to-modern populations who were not interbred with, or iii) already populated with modern (or close-to-modern) humans, with whom the expansion wave reproduced (Henn et al., 2018). The origin of across-Africa expansion is *not* necessarily *the* origin of modern humans (e.g., Bergström et al., 2021; Henn et al., 2018; Rito et al., 2019), and it may have been an early part of the out-of-Africa expansion (e.g., Betti et al., 2012; Hallett et al., 2025; Henn et al., 2012; Manica et al., 2007; Tishkoff et al., 2009). Whilst across-Africa

expansion has received notable attention (e.g., Hallett et al., 2025; Henn et al., 2011), we are unsure if this expansion occurred or where it would have started—the most credible origin is either eastern Africa or southern Africa (e.g., Henn et al., 2018). The present study aimed to shed light on the expansion.

Population bottlenecks and admixture

Expansions, e.g., out-of-Africa or the (Holocene) Bantu expansion (Li et al., 2014; Tishkoff et al., 2009), can be explored through the effects of population bottlenecks (Ramachandran et al., 2005; Semo et al., 2019; Sugden & Ramachandran, 2016), e.g., as expansion progresses farther, genetic drift increases (e.g., Fortes-Lima et al., 2024; Ramachandran et al., 2005; Sugden & Ramachandran, 2016), therefore, within-population genetic diversity decreases and linkage disequilibrium (LD) rises (Jakobsson et al., 2008; Ramachandran et al., 2005; Sugden & Ramachandran, 2016). These diversity/LD patterns occur globally, which is consistent with out-of-Africa expansion (e.g., Jakobsson et al., 2008; Ramachandran et al., 2005). The genetic pattern in diversity is echoed in cranial diversity (Betti et al., 2009; von Cramon-Taubadel & Lycett, 2008).

Admixture affects diversity and LD (Bergström et al., 2021; Haber et al., 2016; Henn et al., 2011), complicating the study of expansion (Colonna et al., 2011; Henn et al., 2011). Diversity and LD have a bottleneck-consistent signal of the Bantu expansion despite this expansion spreading to populated areas and admixture occurring (Fortes-Lima et al., 2024); the Bantu expansion notably changed the genetic landscape of Africa (e.g., Fortes-Lima et al., 2024; Skoglund et al., 2017). Indeed, given demographic changes (migration and admixture), it *is* worth questioning if across-Africa expansion would be detectable (Hunley & Cabana, 2016).

Diversity within continents: Africa

There are doubts regarding within-continent trends in diversity (Bergström et al., 2021; Hunley & Cabana, 2016; Khan, 2020; Schlebusch et al., 2012; Table 1). In an interview, Sohini Ramachandran (of Ramachandran et al., 2005) (Khan, 2020) seems to have been saying that the out-of-Africa heterozygosity decline is not present amongst populations *within* a continent. It is uncertain if genetic diversity and LD indicate across-Africa expansion, possibly because of i) the number of populations used, and ii) the location/point from which we measure geographical distance (Table 1; Cenac, 2022). Nevertheless, *searching* for a point which produces a trend consistent with expansion (e.g., Henn et al., 2011) is problematic, e.g., a trend could appear due to chance (Van Tuyl & Pereltsvaig, 2012). Therefore, it may be useful to explore expansion *across* an array of diversities and datasets to get a holistic impression of where across-Africa expansion originated (e.g., Batini & Jobling, 2011), as the present study did (*Method*).

Table 1

Across-Africa Expansion: Trends?

Study	Variable	Finding
Henn et al. (2011)	Linkage disequilibrium	• Using 25 population datapoints, the across-Africa expansion seemed to have begun in southern-southwestern Africa, e.g., linkage disequilibrium increases with distance from southwestern Africa (Henn et al., 2011). • In later research, a variable found from linkage disequilibrium (Schlebusch et al., 2012) did not indicate a geographical origin (López et al., 2015) (also see the row below).
Schlebusch et al. (2012)	Various	• Haplotype diversity (richness and heterozygosity) did not have a patent geographical pattern, and a regional origin of across-Africa expansion was not suggested through these diversities, runs of homozygosity, and a variable derived from linkage disequilibrium (Schlebusch et al., 2012). • Supplementary material in Schlebusch et al. (2012) indicates that they only used about 20 populations for each variable. Limiting analysis to one continent results in a loss of statistical power when it comes to a bottleneck-consistent signal (Atkinson, 2012). Compared to analyses with populations globally (Prugnolle et al., 2005; Ramachandran et al., 2005), 20 is low. Therefore, Schlebusch et al. (2012) may have had low chances of detecting clear trends. Moreover, sample size affects our ability to delineate origins (Manica et al., 2007); perhaps Schlebusch et al. used too few datapoints.
Hunley and Cabana (2016)	Autosomal gene diversity (i.e., expected heterozygosity, e.g., Luo et al., 2019)	• Autosomal gene diversity had no significant decline with distance from eastern Africa (Hunley & Cabana, 2016). • However, in a preprint, a significant decrease in autosomal heterozygosity was evident when distance was from southern Africa—our ability to detect a pattern in diversity is affected by the point in Africa that we use as the origin of the expansion (Cenac, 2022). Detection of a pattern in linkage disequilibrium is also affected by which *origin* is used (Henn et al., 2011).

Note. Each of the three studies used Holocene data (Henn et al., 2011; Hunley & Cabana, 2016; Schlebusch et al., 2012; Tishkoff et al., 2009; Pemberton et al., 2013).

A previous study, Schlebusch et al. (2012), examined geographical variation in biological variables (listed in Table 1) amongst sub-Saharan Africans. Broadly, these variables did not specify an origin for across-Africa expansion (Schlebusch et al., 2012). However, Schlebusch et al. do not seem

to mention testing for statistically significant trends between these variables and distance from any one location in Africa when it comes to sub-Saharan African populations. Schlebusch et al. appear to have used a visual method for identifying trends and the origin—they showed a map of Africa for each variable, with colours at population locations representing values in biological variables. Judging by results in Fortes-Lima et al. (2024), this method would be insensitive to detecting patterns and an origin. The results: i) a decline in haplotype richness consistent with the Bantu expansion was evident when a statistical test was run, and yet, ii) population diversity levels on maps of Africa (Fortes-Lima et al., 2024), when glanced at, do not readily indicate this pattern. The potential insensitivity in Schlebusch et al. (2012) is compounded by them having used fewer than half as many populations as Fortes-Lima et al. (2024).

Aims

The present study examined the across-Africa expansion through four diversities, each of which exhibits the out-of-Africa expansion pattern of decreasing with distance from Africa: autosomal, cranial shape, mitochondrial, and X-chromosomal diversities (Balloux et al., 2009; von Cramon-Taubadel & Lycett, 2008) (Text S1 explains why phonemic diversity and Y-chromosomal diversity were not used). Largely, diversities were from different datasets (Balloux et al., 2009; Howells, 1989, 1996; Mallick et al., 2016; Manica et al., 2007). Analyses tested for statistically significant geographical patterns in diversity, and searched for the origin indicated by *each* diversity and *across* diversities (*Method*).

Method

In order to analyse data and perform calculations, I utilised R Version 4.0.5 (R Core Team, 2021), RMET 5.0 (Relethford & Blangero, 1990), and Microsoft Excel.

Population samples

Cranial

The present study used cranial data of Holocene modern humans who are sub-Saharan African (Howells, 1989, 1996; Manica et al., 2007) (see Tables S1 and S2); cranial measurements (25 dimensions) were sourced from two datasets which were i) the Howells dataset (Howells, 1973, 1989, 1995, 1996; http://web.utk.edu/~auerbach/HOWL.htm) and ii) data used in Manica et al. (2007). From the literature, the latter dataset can be regarded as a dataset (Betti et al., 2009) whilst being a subset of the broader dataset of Hanihara (Algee-Hewitt, 2011; Betti et al., 2010; Hanihara, 2000, 2008; Hubbe et al., 2009; Manica et al., 2007) which has previously been combined with the Howells dataset along common dimensions (Algee-Hewitt, 2011).

There are duplications between datasets when it comes to Kenya/Teita, San, and Zulu (Algee-Hewitt, 2011); populations from the Howells data were selected in such instances. If Howells and Manica et al. data are combined, there are 13 sub-Saharan African populations with male crania, and only 8 sub-Saharan African populations with female crania. Previous studies have not used males and

females simultaneously when it comes to cranial diversity in form (Betti et al., 2009; Manica et al., 2007) or shape (von Cramon-Taubadel & Lycett, 2008); in the present study, male crania and female crania were not studied simultaneously. In the context of studies on across-Africa expansion (e.g., Henn et al., 2011; Schlebusch et al., 2012), even 13 populations are few. However, with even fewer populations having female crania, only male crania were used. Regarding cranial data, for each population, at least 15 individuals were represented (Howells, 1996; Manica et al., 2007; von Cramon-Taubadel & Lycett, 2008).

Following previous research (Hubbe et al., 2009; von Cramon-Taubadel & Lycett, 2008), cranial shape was found by dividing dimensional measurements by the geometric mean of the cranium. Also, like in preceding research (von Cramon-Taubadel & Lycett, 2008), within-population cranial shape diversity was calculated in RMET 5.0 (Relethford & Blangero, 1990). Additionally, principal coordinates analysis was used in RMET (Relethford & Blangero, 1990) on the cranial shape dimensions.

Genetic

Balloux et al. (2009) analysed mitochondrial DNA, representing the contemporary situation for mitochondrial DNA of modern humans across the planet. The present study specifically used mitochondrial diversity (differences from hypervariable segment 1) in each of 20 sub-Saharan African populations (Balloux et al., 2009). Balloux and colleagues sourced this data from HVRBase++, giving Kohl et al. (2006) as their citation (Balloux et al., 2009). The smallest number of individuals from which mitochondrial diversity was found was 10 (Balloux et al., 2009). There could be good reason to adjust mitochondrial diversity for minimum temperature in the context of out-of-Africa expansion (Cenac, 2022); mitochondrial diversity is correlated with minimum temperature (Balloux et al., 2009), therefore, in this study, mitochondrial diversity was adjusted for minimum temperature in order to better retrieve an expansion signal. Minimum temperatures found in Balloux et al. (2009) were used to control mitochondrial diversity for minimum temperature.

The present study used diversities (expected heterozygosity derived from base pair variation) of contemporary modern human populations which Mallick et al. (2016) calculated from Simons Genome Diversity Project data. These diversities were X-chromosomal (males in 17 sub-Saharan African populations) and autosomal (20 sub-Saharan African populations) (Mallick et al., 2016). X-chromosomal diversity was used for males alone because inspection of the Mallick et al. (2016) data suggested sexual dimorphism in X-chromosomal diversity, and X-chromosomal diversity was available in more sub-Saharan African populations for males than females in the dataset from Mallick et al. (2016). Regarding X-chromosomal and autosomal diversities, in instances where more than one individual was present for a population, a mean was calculated and used for that population. For these two diversities, populations were each represented by as few as one person (Mallick et al., 2016; see Table S3), which, compared to previous research on diversity/LD and out-of-Africa/across-Africa expansion (Balloux et al., 2009; Henn et al., 2011; Manica et al., 2007) is very low. In a previous

publication, neither X-chromosomal nor autosomal diversity (each adjusted for distance from Africa) had an association with minimum temperature (Balloux et al., 2009). Therefore, in the present study, neither diversity was controlled for minimum temperature (but, see *Discussion*). To minimise the influence of non-African gene flow, analysis can be restricted to sub-Saharan African populations (Cenac, 2022), and that practice was applied in the current study for cranial and genetic diversities.

Geographical distances

Regarding the Manica et al. data, based on previous research (Betti et al., 2009; Hubbe et al., 2009; Manica et al., 2007), populations were matched to geographical coordinates presented in Hubbe et al. (2009); these coordinates were used as the locations of the Manica et al. populations. As for the Howells data, preceding research assigned coordinates to populations (von Cramon-Taubadel & Lycett, 2008), and those coordinates were used in the present study. Regarding genetic diversities, population coordinates were used from Balloux et al. (2009) and Mallick et al. (2016). Geographical distances were obtained from elsewhere (Cenac, 2022) or they were calculated using the methodology of Williams (2011)—these distances were calculated i) between 99 mainland African locations (which Betti et al., 2013, employed, each as an *origin* in research on out-of-Africa expansion) and population coordinates, and ii) between population coordinates. Hence, in the current study, analysis used the mainland African locations like they were *origins*.

Origin estimation

Following prior research, the range of geographical coordinates which hosts the origin of expansion was inferred through the Bayesian information criterion (BIC)—this was done by identifying i) the *origin* which generated the strongest decline of diversity (with distance), as indicated by the location which provides the lowest BIC, and ii) other origins which each produce a decline of a similar strength to the greatest decline (less than four BICs above the lowest) (e.g., Atkinson, 2011; Cenac, 2022; Manica et al., 2007). A formula (Masson, 2011) was employed to calculate BICs, or BICs were calculated in R. Southern Africa was defined following Choudhury et al. (2021). A ranking procedure has been used in a preprint in order to obtain a general impression of where the expansion began; in that procedure, i) correlation coefficients are calculated for individual African *origins*, and the coefficients are ranked for each type of genetic diversity, ii) for each origin, an average of the ranks is determined, iii) the averages are re-ranked across locations, and iv) the ranks are represented on a map of mainland Africa (Cenac, 2023a)—that method was used in the present study i) to get a general idea of the origin from genetic diversities, ii) to estimate the origin from genetic diversities and (overall) cranial shape diversity, and iii) for an impression of where cranial shape dimensions suggest the origin is. The design of Figures 1D, 2A, 2C, 2D, 3A, 3B, S1, and S2 have a basis in the designs of figures in preprints, Cenac (2022; 2023a), which have some basis on a figure from Betti et al. (2013).

Correlation and spatial autocorrelation

When it came to understanding if there are significant declines in diversity with distance (from a location), the location generating the lowest BIC was used—this method has been employed with phonemic diversity for instance (Atkinson, 2011), and it was applied in correlation analyses (and post-hoc regression analysis—Text S2) analyses in the current study. A location could possess the greatest relationship between phonemic diversity and geographical distance for a number of reasons, even chance (Van Tuyl & Pereltsvaig, 2012); basing a significance test on the greatest decline (e.g., Atkinson, 2011; Figure 1C) is flawed, essentially skewing analysis towards *finding* a significant correlation. This is a reason for why it is important to see if measures *generally* agree on the origin. For a datapoint to be deemed atypical, it was required to have a standardised residual surpassing |3.29| (e.g., Field, 2013) in the present analyses. When testing if mitochondrial diversity (adjusted for minimum temperature) correlates with geographical distance, Kim's (2015) ppcor package was used to run a semi-partial Pearson correlation test. A Holm-Bonferroni correction was applied to *p*-values from correlation and regression tests (Gaetano, 2013; Holm, 1979). Positive spatial autocorrelation was tested for (amongst residuals), which involved the spatial Durbin-Watson (*DW*) statistic (Chen, 2016; Savin & White, 1977).

Results

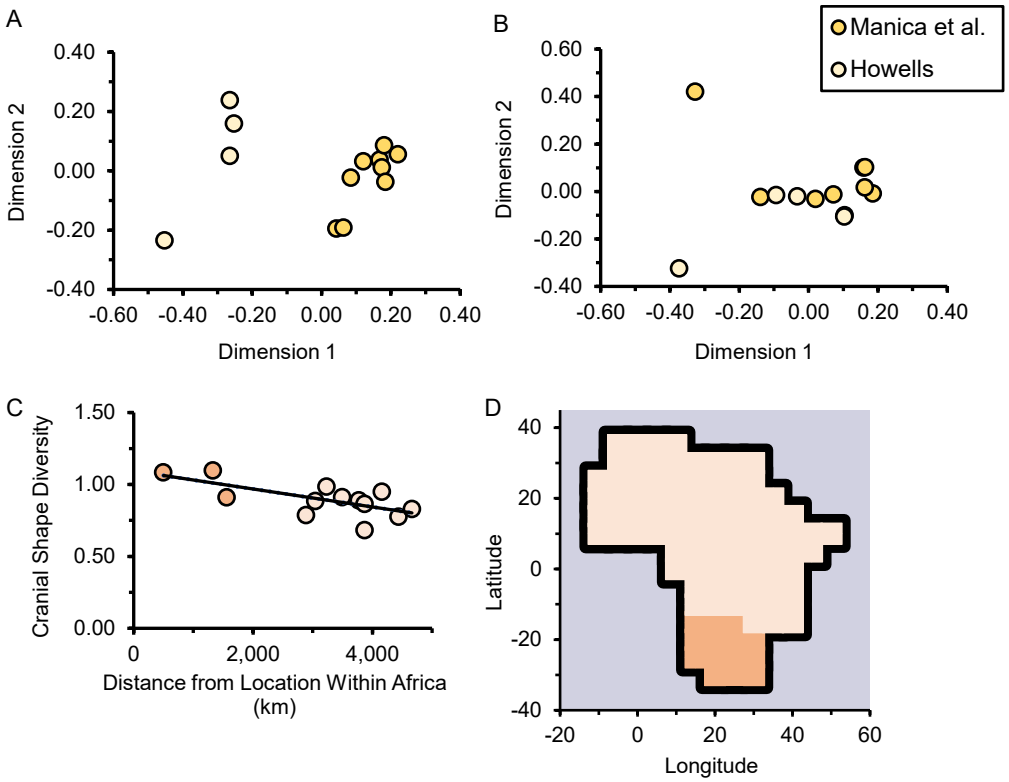
Cranial shape diversity

Cranial shape diversity was calculated from two datasets: Howells (e.g., 1989, 1996) and Manica et al. (2007). When cranial shape was calculated using 25 dimensions (Table S2), principal coordinates analysis indicated a difference between datasets (Figure 1A). Manica et al. data are from the Hanihara dataset (e.g., Algee-Hewitt, 2011; Betti et al., 2010; Manica et al., 2007). The *name* of a dimension can be common to Howells and Hanihara data without the dimension *itself* being the same—there are discrepancies in how cranial locations are defined (Algee-Hewitt, 2011). So, discrepancies (Algee-Hewitt, 2011) likely explain why cranial shape seems to differ between datasets. When combining Howells and Hanihara data, 11 dimensions are known to not give an issue (Algee-Hewitt, 2011); no issue was indicated for those dimensions (Table S2) regarding cranial shape (Figure 1B), therefore, analyses proceeded using those dimensions alone.

As distance from southern Africa (25°S, 15°E) increased, there was a fall in cranial shape diversity, $r(11) = -.68$, $p = .040$, spatial $DW = 2.41$ (Figure 1C). Southern Africa was identified as the most likely origin for the across-Africa expansion because the strongest declines were when distance was from any one of various locations in southern Africa (Figure 1D). Cranial dimensions differ in how much they capture out-of-Africa expansion (Betti et al., 2009; Cenac, 2022); the application of a ranking procedure (see *Method*) did not indicate that a small proportion of the dimensions drove results (Figure S1; Table S2).

Figure 1

Cranial Shape Diversity: A Southern African Origin for Across-Africa expansion?



Note. Figure 1A and 1B represent dimensions from principal coordinates analysis. In Figure 1A and 1B, regions of Africa are signified by different colours. In Figure 1A, Dimensions 1 and 2 respectively captured 50.3% and 19.0% of the interpopulation variation in cranial shape. Dimension 1 separated the Howells data (less than -.20) from the Manica et al. (2007) data (above 0.00). In Figure 1B, Dimension 1 covered 44.8% of the variation, whilst Dimension 2 covered 35.4%, and neither dimension seemed to distinguish between the Howells and Manica et al. data. Figure 1C presents the decrease in cranial shape diversity. In Figure 1D, the area of Africa with darker shading is the area amongst which the expansion is suggested to have originated.

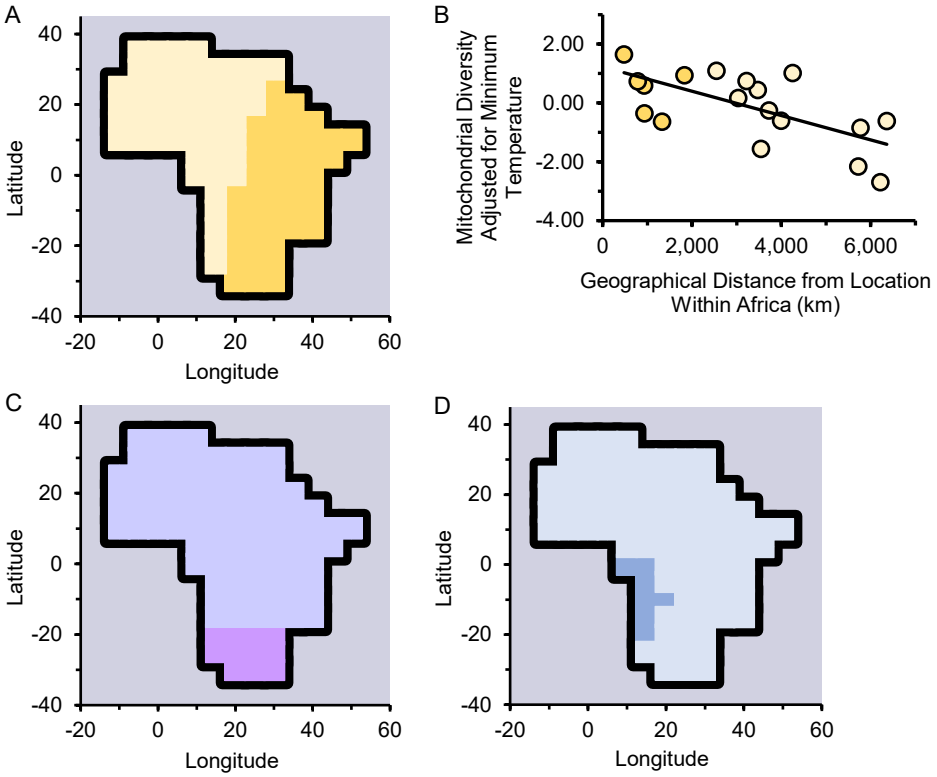
Genetic diversities, and the origin indicated across diversities

Genetic diversities (Balloux et al., 2009; Mallick et al., 2016) exhibited a pattern within sub-Saharan Africa (e.g., Figure 2). Mitochondrial diversity, adjusted for minimum temperature (see *Method*), decreased with distance from eastern Africa (5°N, 40°E), $r(17) = -.68$, $p = .006$, spatial *DW* = 2.17 (Figure 2B), however, no particular region was singled out as the origin (Figure 2A). X-chromosomal diversity declined as geographical distance from southern Africa (30°S, 25°E) rose, $r(15) = -.57$, $p = .043$, spatial *DW* = 2.11, and a southern African origin was indicated (Figure 2C). Autosomal diversity exhibited a decline with distance from (10°S, 15°E), $r(18) = -.54$, $p = .043$, spatial *DW* = 2.05, and indicated an origin somewhere in an area which crossed the regions of southern and central Africa (Figure 2D). Positive spatial autocorrelation was not observed regarding analysis with cranial diversity or genetic diversities. When considering the genetic diversities

concurrently, a southern origin was indicated (Figure 3A), and this indication persisted when cranial shape diversity was added (Figure 3B).

Figure 2

Genetic Diversity and the Origin of Across-Africa Expansion.

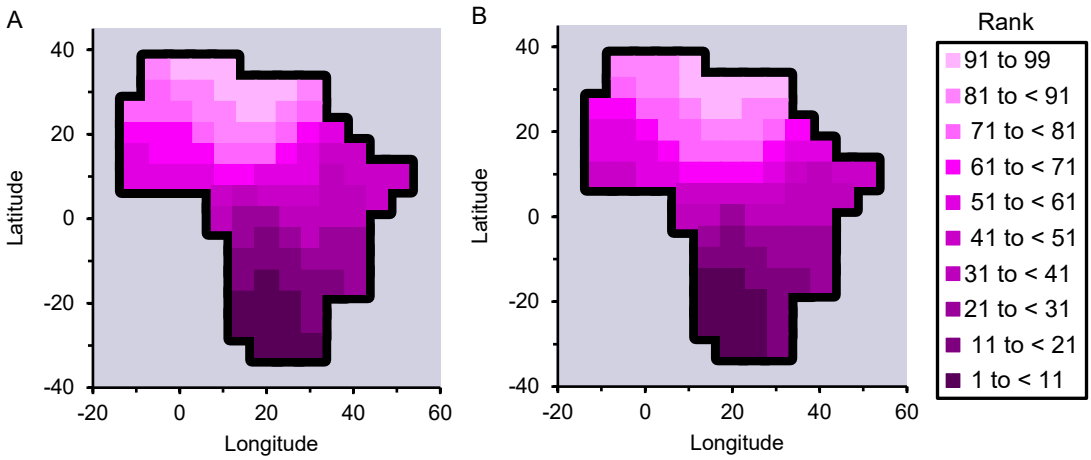


Note. Figure 2A and 2B are regarding (adjusted) mitochondrial diversity, whilst Figure 2C and 2D are regarding X-chromosomal diversity and autosomal diversity respectively. In each map, the darker-shaded area indicates a geographical area amongst which the across-Africa expansion originated (Figures 2A, 2C, and 2D).

When it came to autosomal diversity, the datapoint for the Somali population (Mallick et al., 2016) overly affected results. In terms of standardised residuals, the datapoint was not atypical (z = -2.75) given that |3.29| was used as the cutoff (*Method*). Clearly, this would have been regarded as atypical if a more stringent cutoff, such as |1.96| (Field, 2013), was used. To be cautious, studentized deleted residuals were calculated post-hoc using the MASS package (Venables & Ripley, 2002) in R. The Somali population had a studentized deleted residual of -4.72. This suggested (e.g., Judd et al., 2009) that the Somali datapoint had a considerable effect on results. Indeed, in the absence of the datapoint, the correlation coefficient (r) was only -.24 (rather than the r-value of -.54 found in their presence). Crucially, without the datapoint, BICs (alone) no longer distinguished a set of possible origins regarding across-Africa expansion. When autosomal diversity was excluded from the overall estimate of the origin, a southern origin was still indicated (Figure S2).

Figure 3

Estimating the Origin of Across-Africa Expansion Across Diversities.



Note. The higher the rank, the more support there is for a location being the origin of the across-Africa expansion. Figure 3A uses three genetic diversities: mitochondrial adjusted for minimum temperature, X-chromosomal, and autosomal. Figure 3B uses those genetic diversities, supplemented by cranial shape diversity.

Discussion

On the whole, correlations were strong (Cohen, 1992) regarding relationships between diversity and geographical distance. This is contrary to some stances (e.g., Bergström et al., 2021; Schlebusch et al., 2012) in the literature. Now, it is clear that diversity within Africa is compatible with an across-Africa expansion. Whilst southern and eastern Africa are the most promising options for the origin (Henn et al., 2018), the current study emphasizes the south (Figure 3). A previous study found that different measures did not generally mark out an origin (Schlebusch et al., 2012). However, as covered in the *Introduction*, that study may not have used a methodology which was sufficiently sensitive. If across-Africa expansion is contiguous with the broader out-of-Africa expansion (Hallett et al., 2025; Henn et al., 2018), then examining out-of-Africa expansion may suggest the origin of across-Africa expansion (Tishkoff et al., 2009), particularly as African populations have a substantial effect on estimating the origin of out-of-Africa expansion; an estimate of southern Africa was found in a preprint which concurrently used genetic diversities, cranial shape diversity, and cranial sexual size dimorphism (Cenac, 2022). That estimate aligns with the present study (e.g., Figure 3).

Admixture

Admixture is an issue for identifying the origin of the across-Africa expansion (e.g., Colonna et al., 2011). It is next considered if this issue was addressed by the current study. A bottleneck-congruent expansion pattern (e.g., the decrease of diversity) may, to some extent, reflect events which happened after expansion—later migration and admixture (e.g., Skoglund & Mathieson, 2018). Such travel and admixture can affect our ability to estimate the origin of the across-Africa expansion (e.g., Colonna et al., 2011). Admixture increases diversity (Bergström et al., 2021) usually, although not necessarily (Haber et al., 2016). Admixture also increases LD (Henn et al., 2011). With distance from

the supposed origin, diversity declines (e.g., Betti et al., 2009; Ramachandran et al., 2005), whilst LD increases (e.g., Henn et al., 2011). Therefore, bottlenecks and admixture typically affect diversity in *different* directions, whilst they affect LD in the *same* direction. Hence, whilst admixture may affect the origin estimated by diversity and by LD (Bergström et al., 2021; Henn et al., 2011), admixture would have the *opposite* effect on origin estimation when we use diversity than when we use LD. Consequently, the occurrence of a southern origin being indicated by LD in Henn et al. (2011) suggests that admixture is not the reason for a southern origin being found in the present study. On the other hand, a variable derived from LD (Schlebusch et al., 2012) was unable to suggest any origin (López et al., 2015), however, only about 20 populations were used (Schlebusch et al., 2012; see Table 1). Moreover, the research was Schlebusch et al. (2012), and, as noted above, their method for indicating origins may not have been sensitive.

Considering Khoe-San

If the across-Africa expansion started in the south, then we might expect an indication that Khoe-San were involved early in the expansion (e.g., Henn et al., 2012) because they are longstanding southern African populations (Henn et al., 2012; Hodgson et al., 2014; Schlebusch et al., 2020; Skoglund et al., 2017). Nonetheless, it is still acknowledged that the geographical range of southern Khoe-San-linked ancestry stretched from the south to part of *eastern* Africa before the Bantu expansion (Skoglund et al., 2017). High diversity and low LD characterise the origin of expansion (e.g., Henn et al., 2011; Ramachandran et al., 2005), and, amongst Africans, Khoe-San are known to be i) high in genetic diversity even when analysis addresses their recent admixture (Schlebusch et al., 2020), and ii) low in LD (Henn et al., 2011). Diversity and LD are not the only modes of examining the existence/origin of expansion (e.g., Henn et al., 2011; Li et al., 2008). Other (actual/potential) methods (e.g., Bergström et al., 2021; Cole et al., 2020; Ragsdale et al., 2023) collectively bring doubt to early Khoe-San involvement (Table 2).

Limitations

Drawing on the literature (e.g., Amos, 2020; Balloux, 2009; Manica et al., 2007), a number of limitations to this study are considered, centring on i) admixture, ii) the absence of southern African populations when it comes to mitochondrial diversity, and iii) X-chromosomal diversity and climate.

Admixture: Addressing a broad effect?

Research on the Bantu expansion (regarding diversity and distance) has included masking out parts of the genome (admixture) so that only relevant ancestral components (western-central African) are used in certain analyses (Fortes-Lima et al., 2024) (also see Henn et al., 2011, who attempted to explore across-Africa expansion using a genetic distance measure, lessening an impact of gene flow from Europeans). A similar approach could be used regarding across-Africa expansion in order to reduce any effect of admixture. Nonetheless, trends of a gradual decline in diversity and increase in LD can be found *without* an expansion occurring, e.g., if *some* established populations went through substantial bottlenecks and admixing subsequently occurred (Pickrell & Reich, 2014). Therefore, to

understand the history of modern humans in Africa, it is important that we rigorously examine scenarios beyond expansion (e.g., Ragsdale et al., 2023), which the present study did not do.

Table 2

Across-Africa Expansion: Qualities Outside of Diversity and Linkage Disequilibrium?

Quality	Outcomes
Predecessors of Eurasians	• A preprint indicated gene flow into Africans, 40-to-70 thousand years before present, from predecessors of Eurasians (who were without Neanderthal admixture) (Cole et al., 2020); this *could* be the across-Africa expansion (Bergström et al., 2021). • Ancestry from these predecessors, which could be highest at the origin (Bergström et al., 2021), is lowest in Khoe-San (amongst Africans) (Cole et al., 2020), contrary to a southern origin.
Divergence?	• For extant groups, the earliest divergence in a phylogenetic tree differentiates Khoe-San from non-Khoe-San (e.g., Li et al., 2008; Schlebusch et al., 2020), which seems to have been implied (e.g., in Henn et al., 2012) to agree with a southern origin. • Early divergence was not suggested in a study using a maximum-likelihood procedure and incorporating gene flow—distinct of Khoe-San, a combining of ancestral central/western and ancestral eastern Africans apparently produced ancestors of non-Khoe-San, however, ancestral labels were shaped by current population locations, and contemporary southern and western Africa were each denoted by one population (Ragsdale et al., 2023). • Across studies using maximum-likelihood procedures, there is considerable variation in patterns regarding ancient human history, possibly because of a large part of a continent being spoken for by one population (Breton et al., 2024).
Effective population size	• Effective population size falls with distance from Africa, corresponding to expansion through bottlenecks (Li et al., 2008). • Africans are indicated to have declined in effective population size approximately 100,000 years ago, to various extents, with Khoe-San impacted least (Schlebusch et al., 2020). Given the timing (Henn et al., 2012), this agrees with the pre-Bantu-expansion geographical range of Khoe-San-linked ancestry (Skoglund et al., 2017) being the origin of across-Africa expansion. The decline *could* be attributable to climate (Schlebusch et al., 2020), however, it could be that climate triggered out-of-Africa expansion (Tierney et al., 2017).

Admixture: Eurasian ancestry

In analysis with autosomal diversity, the Somali datapoint affected results. Why is that? Eurasian gene flow seems to decrease African genetic diversity (Haber et al., 2016). Around 40% of

Somali ancestry is Eurasian (Haber et al., 2016; Pickrell et al., 2014). Compared to other sub-Saharan African populations (Haber et al., 2016; Pickrell et al., 2014; Tishkoff et al., 2009), that percentage is relatively high. As for Somalis specifically in the data used in the current study (regarding autosomal diversity), who were only represented by one individual, the population is highest in Neanderthal ancestry (Mallick et al., 2016). Africans acquired Neanderthal ancestry due to gene flow from non-Africans (Chen et al., 2020)—the level of Neanderthal ancestry for Somalis (Mallick et al., 2016) is congruent with a relatively high Eurasian ancestry. However, there is reason to be cautious over archaic ancestry levels (e.g., Amos, 2020, 2021, n.d.; Skoglund & Jakobsson, 2011); a reduction in heterozygosity may have lessened mutation rate, therefore, less diverse populations may diverge less from the common ancestor shared by modern humans, consequently, diverging less from archaic humans (Amos, 2021). Indeed, for Eurasians, Neanderthal ancestry greatens with distance from Africa (Amos, 2021). And yet, the greater Neanderthal ancestry in eastern Eurasia than western Eurasia may be attributable to population movement around 10,000 years ago—before then, western Eurasians do not appear to have had lower Neanderthal ancestry than eastern Eurasians (Quilodrán et al., 2023). Hence, the loss of heterozygosity (Amos, 2021) may not have affected supposed archaic ancestry levels. Therefore, Neanderthal ancestry may indicate that results regarding autosomal diversity were affected by Eurasian ancestry.

Nevertheless, for autosomal diversity, the largest negative correlation coefficient was at the same location regardless of whether the Somali datapoint was included (Figure S3). Moreover, comparing when the datapoint was, and was not, included, there seems to be a broad agreement in how relatively well locations each functioned as the origin (Figure S3). Therefore, it could be that i) autosomal diversity has an actual across-Africa expansion trend, or ii) results were merely driven by Eurasian ancestry, or iii) results were due to a combination of the across-Africa signal alongside Eurasian ancestry. Consequently, it may be crucial that, in analysis with sub-Saharan Africans, we adjust for non-African admixture, however, in a preprint where such an adjustment was made, autosomal microsatellite heterozygosity indicated a southern origin (Cenac, 2022).

Mitochondrial diversity: Absence of southern populations

Mitochondrial diversity points to a noticeably larger geographical range of possible origins than cranial and X-chromosomal diversities (Figures 1 and 2). Southern Africa was not represented in mitochondrial diversity (Balloux et al., 2009), unlike the other diversities (Howells, 1989; Mallick et al., 2016; Manica et al., 2007; von Cramon-Taubadel & Lycett, 2008). Given the methodology used for estimating the origin (e.g., Manica et al., 2007; see *Method*), mitochondrial diversity may have given a less precise estimate.

X-chromosomal diversity and climate

X-chromosomal diversity was not adjusted for minimum temperature. Was this wise? Whilst a previous publication did not find a relationship between X-chromosomal diversity (adjusting for distance from Africa) and minimum temperature (Balloux et al., 2009), a subsequent preprint found an

association by furthering the analysis from that publication—adjusted diversity *greatened* with minimum temperature (Cenac, 2023b). So, given climate in sub-Saharan Africa, wherein the south is relatively cool (Balloux et al., 2009; Glunt et al., 2013), it seems unlikely that X-chromosomal diversity indicated a southern origin (Figure 2C) because of climate, and the current study may have actually underestimated the strength of the across-Africa expansion signal in X-chromosomal diversity.

Conclusion

When it comes modern human history in Africa, two questions are: i) does diversity have a geographical pattern within African populations, declining from a geographical point within Africa, and ii) *if* there is a pattern, what does it mean (e.g., Hunley & Cabana, 2016; Schlebusch et al., 2012)? It is now clear that, broadly, there are trends in the diversity of sub-Saharan Africans which are consistent with across-Africa expansion (Figures 1 and 2; Table 1). It is also clear that trends generally suggest an expansion from southern Africa (Figure 3; Figure S2). Linkage disequilibrium may indicate an origin which is similar (Henn et al., 2011; cf. López et al., 2015; Schlebusch et al., 2012) to what diversity generally suggests (e.g., Figure 3). Therefore, findings in this study could, to some level, help address a broad effect of admixture on the estimation of the origin, however, the effect of admixture could be addressed more thoroughly (*Admixture*). Moreover, it is questionable if Khoe-San were involved early in this expansion (Table 2), which means it is also questionable if trends in diversity (e.g., Figures 1 and 2) actually are a product of the expansion.

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References

Algee-Hewitt, B. F. B. (2011). *If and how many 'races'? The application of mixture modeling to world-wide human craniometric variation* [Doctoral dissertation, The University of Tennessee, Knoxville]. Tennessee Research and Creative Exchange. https://trace.tennessee.edu/utk_graddiss/1165/

Amos, W. (2020). Signals interpreted as archaic introgression appear to be driven primarily by faster evolution in Africa. *Royal Society Open Science*, *7*(7), Article 191900. https://doi.org/10.1098/rsos.191900

Amos, W. (2021). Correlated and geographically predictable Neanderthal and Denisovan legacies are difficult to reconcile with a simple model based on inter-breeding. *Royal Society Open Science*, *8*(6), Article 201229. https://doi.org/10.1098/rsos.201229

Amos, W. (n.d.). *Is the idea that many humans carry some Neanderthal DNA correct?* https://www.zoo.cam.ac.uk/files/media/the_question_of_neanderthal_inter-breeding.docx

Atkinson, Q. D. (2011). Phonemic diversity supports a serial founder effect model of language expansion from Africa. *Science*, *332*(6027), 346–349. https://doi.org/10.1126/science.1199295

Atkinson, Q. D. (2012). Response to comments on "Phonemic Diversity Supports a Serial Founder Effect Model of Expansion from Africa". *Science*, *335*(6069), Article 657-e. https://doi.org/10.1126/science.1210005

Balloux, F., Lawson Handley, L.-J., Jombart, T., Liu, H., & Manica, A. (2009). Climate shaped the worldwide distribution of human mitochondrial DNA sequence variation. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1672), 3447–3455. https://doi.org/10.1098/rspb.2009.0752

Batini, C., & Jobling, M. A. (2011). The jigsaw puzzle of our African ancestry: Unsolved, or unsolvable? *Genome Biology*, *12*(6), Article 118. https://doi.org/10.1186/gb-2011-12-6-118

Bergström, A., Stringer, C., Hajdinjak, M., Scerri, E. M. L., & Skoglund, P. (2021). Origins of modern human ancestry. *Nature*, *590*, 229–237. https://doi.org/10.1038/s41586-021-03244-5

Betti, L., Balloux, F., Amos, W., Hanihara, T., & Manica, A. (2009). Distance from Africa, not climate, explains within-population phenotypic diversity in humans. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1658), 809–814. https://doi.org/10.1098/rspb.2008.1563

Betti, L., Balloux, F., Hanihara, T., & Manica, A. (2010). The relative role of drift and selection in shaping the human skull. *American Journal of Physical Anthropology*, *141*(1), 76–82. https://doi.org/10.1002/ajpa.21115

Betti, L., von Cramon-Taubadel, N., & Lycett, S. J. (2012). Human pelvis and long bones reveal differential preservation of ancient population history and migration out of Africa. *Human Biology*, *84*(2), 139–152. https://doi.org/10.3378/027.084.0203

Betti, L., von Cramon-Taubadel, N., Manica, A., & Lycett, S. J. (2013). Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes. *PLoS ONE*, *8*(2), Article e55909. https://doi.org/10.1371/journal.pone.0055909

Breton, G., Sjödin, P., Zervakis, P. I., Laurent, R., Froment, A., Sjöstrand, A. E., Hewlett, B. S., Barreiro, L. B., Perry, G. H., Soodyall, H., Heyer, E., Schlebusch, C. M., Jakobsson, M., & Verdu, P. (2024). *Ancient tree-topologies and gene-flow processes among human lineages in Africa*. bioRxiv. https://doi.org/10.1101/2024.07.15.603519

Cabrera, V. M. (2022). Following the evolution of *Homo Sapiens* across Africa using a uniparental genetic guide. *Medical Research Archives*, *11*(1). https://doi.org/10.18103/mra.v11i1.3460

Cenac, Z. (2022). *Modern human expansion from (southern?) Africa: Origin, non-African ancestry, and linearity*. bioRxiv. https://doi.org/10.1101/2022.07.31.500977

Cenac, Z. (2023a). *Y-chromosomal microsatellites and expansion from Africa*. bioRxiv. https://doi.org/10.1101/2023.04.29.538812

Cenac, Z. (2023b). *X-chromosomal diversity may reflect climate (when considering human expansion from Africa)*. bioRxiv. https://doi.org/10.1101/2023.09.15.557915

Chen, L., Wolf, A. B., Fu, W., Li, L., Akey, J. M. (2020). Identifying and interpreting apparent Neanderthal ancestry in African individuals. *Cell*, *180*(4). 677-687.e16 https://doi.org/10.1016/j.cell.2020.01.012

Chen, Y. (2016). Spatial autocorrelation approaches to testing residuals from least squares regression. *PLoS ONE*, *11*(1), Article e0146865. https://doi.org/10.1371/journal.pone.0146865

Choudhury, A., Sengupta, D., Ramsay, M., & Schlebusch, C. (2021). Bantu-speaker migration and admixture in southern Africa. *Human Molecular Genetics*, *30*(2), R56–R63. https://doi.org/10.1093/hmg/ddaa274

Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*(1), 155–159. https://doi.org/10.1037/0033-2909.112.1.155

Cole, C. B., Zhu, S. J., Mathieson, I., Prüfer, K., & Lunter, G. (2020). *Ancient admixture into Africa from the ancestors of non-Africans*. bioRxiv. https://doi.org/10.1101/2020.06.01.127555

Colonna, V., Pagani, L., Xue, Y., & Tyler-Smith, C. (2011). A world in a grain of sand: Human history from genetic data. *Genome Biology*, *12*, Article 234. https://doi.org/10.1186/gb-2011-12-11-234

Field, A. (2013). *Discovering statistics using IBM SPSS statistics (4th ed.)*. Sage.

Fortes-Lima, C. A., Burgarella, C., Hammarén, R. Eriksson, A., Vicente, M., Jolly, C., Semo, A., Gunnink, H., Pacchiarotti, S., Mundeke, L., Matonda, I., Muluwa, J. K., Coutros, P., Nyambe, T. S., Cikomola, J. C., Coetzee, V., de Castro, M., Ebbesen, P., Delanghe, J., … Schlebusch, C. M. (2024). The genetic legacy of the expansion of Bantu-speaking peoples in Africa. *Nature*, *625*, 540–547. https://doi.org/10.1038/s41586-023-06770-6

Gaetano, J. (2013). *Holm-Bonferroni sequential correction: An EXCEL calculator*. https://www.researchgate.net/publication/236969037_Holm-Bonferroni_Sequential_Correction_An_EXCEL_Calculator

Glunt K. D., Blanford J. I., & Paaijmans K. P. (2013). Chemicals, climate, and control: Increasing the effectiveness of malaria Vector control tools by considering relevant temperatures. *PLoS Pathogens*, *9*(10), Article e1003602. https://doi.org/10.1371/journal.ppat.1003602

Haber, M., Mezzavilla, M., Bergström, A., Prado-Martinez, J., Hallast, P., Saif-Ali, R., Al-Habori, M., Dedoussis, G., Zeggini, E., Blue-Smith, J., Wells, R. S., Xue, Y., Zalloua, P. A., & Tyler-Smith, C. (2016). Chad genetic diversity reveals an African history marked by multiple Holocene Eurasian migrations. *The American Journal of Human Genetics*, *99*(6), 1316-1324. https://doi.org/10.1016/j.ajhg.2016.10.012

Hallett, E. Y., Leonardi, M., Niccolò Cerasoni, J., Will, M., Beyer, R., Krapp, M., Kandel, A. W., Manica, A., & Scerri, E. M. L. (2025). Major expansion in the human niche preceded out of Africa dispersal. *Nature*. https://doi.org/10.1038/s41586-025-09154-0

Hanihara, T. (2000). Frontal and facial flatness of major human populations. *American Journal of Physical Anthropology*, *111*(1), 105–134.

Hanihara, T. (2008). Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology*, *136*(2), 169–182. https://doi.org/10.1002/ajpa.20792

Henn, B. M., Cavalli-Sforza, L. L., & Feldman, M. W. (2012). The great human expansion. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(44), 17758–17764. https://doi.org/10.1073/pnas.1212380109

Henn, B. M., Gignoux, C. R., Jobin, M., Granka, J. M., Macpherson, J. M., Kidd, J. M., Rodríguez-Botigué, L., Ramachandran, S., Hon, L., Brisbin, A., Lin, A. A., Underhill, P. A., Comas, D., Kidd, K. K., Norman, P. J., Parham, P., Bustamante, C. D., Mountain, J. L., & Feldman, M. W. (2011). Hunter-gatherer genomic diversity suggests a southern African origin for modern humans. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(13), 5154–5162. https://doi.org/10.1073/pnas.1017511108

Henn, B. M., Steele, T. E., & Weaver, T. D. (2018). Clarifying distinct models of modern human origins in Africa. *Current Opinion in Genetics & Development*, *53*, 148–156. https://doi.org/10.1016/j.gde.2018.10.003

Hodgson, J. A., Mulligan, C. J., Al-Meeri, A., & Raaum, R. L. (2014). Early back-to-Africa migration into the Horn of Africa. *PLoS Genetics*, *10*(6), Article e1004393. https://doi.org/10.1371/journal.pgen.1004393

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*(2), 65–70.

Howells, W. W. (1973). *Cranial variation in man: A study by multivariate analysis of patterns of difference among recent human populations*. *Papers of the Peabody Museum of Archaeology and Ethnology Volume 67*. Harvard University.

Howells, W. W. (1989). *Skull shapes and the map: Craniometric analyses in the dispersion of Modern Homo. Papers of the Peabody Museum of Archaeology and Ethnology Volume 79*. Harvard University.

Howells, W. W. (1995). *Who's who in skulls: Ethnic identification of crania from measurements. Papers of the Peabody Museum of Archaeology and Ethnology Volume 82*. Harvard University.

Howells, W. W. (1996). Howells' craniometric data on the internet. *American Journal of Physical Anthropology*, *101*(3), 441–442. https://doi.org/10.1002/ajpa.1331010302

Hubbe, M., Hanihara, T., & Harvati, K. (2009). Climate signatures in the morphological differentiation of worldwide modern human populations. *The Anatomical Record*, *292*(11), 1720–1733. https://doi.org/10.1002/ar.20976

Hublin, J.-J., Ben-Ncer, A., Bailey, S. E., Freidline, S. E., Neubauer, S., Skinner, M. M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., & Gunz, P. (2017). New fossils from Jebel Irhoud,

Morocco and the pan-African origin of *Homo sapiens*. *Nature*, *546*, 289–292. https://doi.org/10.1038/nature22336

Hunley, K. L., & Cabana, G. S. (2016). Beyond serial founder effects: The impact of admixture and localized gene flow on patterns of regional genetic diversity. *Human Biology*, *88*(3), 219–231. https://doi.org/10.13110/humanbiology.88.3.0219

Jakobsson, M., Scholz, S. W., Scheet, P., Gibbs, J. R., VanLiere, J. M., Fung, H.-C., Szpiech, Z. A., Degnan, J. H., Wang, K., Guerreiro, R., Bras, J. M., Schymick, J. C., Hernandez, D. G., Traynor, B. J., Simon-Sanchez, J., Matarin, M., Britton, A., van de Leemput, J., Rafferty, I., ... Singleton, A. B. (2008). Genotype, haplotype and copy-number variation in worldwide human populations. *Nature*, *451*, 998–1003. https://doi.org/10.1038/nature06742

Judd, C. M., McClelland, G. H., & Ryan, C. S. (2009). *Data analysis: A model comparison approach*. Routledge.

Khan, R. (Host). (2020, March 11). Decreasing genetic diversity with distance from Africa [Audio podcast episode]. In *the Insight*. Insitome. https://podcasts.apple.com/us/podcast/decreasing-genetic-diversity-with-distance-from-africa/id1324744423?i=1000468138776

Kim, S. (2015). ppcor: An R package for a fast calculation to semi-partial correlation coefficients. *Communications for Statistical Applications and Methods*, *22*(6), 665–674. https://doi.org/10.5351/CSAM.2015.22.6.665

Kohl, J., Paulsen, I., Laubach, T., Radtke, A., von Haeseler, A. (2006). HvrBase++: A phylogenetic database for primate species. *Nucleic Acids Research*, *34*(Database Issue), D700–D704. https://doi.org/10.1093/nar/gkj030

Li, J. Z., Absher, D. M., Tang, H., Southwick, A. M., Casto, A. M., Ramachandran, S., Cann, H. M., Barsh, G. S., Feldman, M., Cavalli-Sforza, L. L., & Myers, R. M. (2008). Worldwide human relationships inferred from genome-wide patterns of variation. *Science*, *319*(5866), 1100–1104. https://doi.org/10.1126/science.1153717

Li, S., Schlebusch, C., & Jakobsson, M. (2014). Genetic variation reveals large-scale population expansion and migration during the expansion of Bantu-speaking peoples. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), Article 20141448. https://doi.org/10.1098/rspb.2014.1448

López, S., van Dorp, L., & Hellenthal, G. (2015). Human dispersal out of Africa: A lasting debate. *Evolutionary Bioinformatics Online*, *11*(S2), 57–68. https://doi.org/10.4137/EBO.S33489

Luo, Z., Brock, J., Dyer, J. M., Kutchan, T., Schachtman, D., Augustin, M., Ge, Y., Fahlgren, N., Abdel-Haleem, H. (2019). Genetic diversity and population structure of a *Camelina sativa* spring panel. *Frontiers in Plant Science*, *10*, Article 184. https://doi.org/10.3389/fpls.2019.00184

Mallick, S., Li, H., Lipson, M., Mathieson, I., Gymrek, M., Racimo, F., Zhao, M., Chennagiri, N., Nordenfelt, S., Tandon, A., Skoglund, P., Lazaridis, I., Sankararaman, S., Fu, Q., Rohland, N., Renaud, G., Erlich, Y., Willems, T., Gallo, C., … Reich, D. (2016). The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature*, *538*, 201–206. https://doi.org/10.1038/nature18964

Manica, A., Amos, W., Balloux, F., & Hanihara, T. (2007). The effect of ancient population bottlenecks on human phenotypic variation. *Nature*, *448*, 346–348. https://doi.org/10.1038/nature05951

Masson, M. E. J. (2011). A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. *Behavior Research Methods*, *43*, 679–690. https://doi.org/10.3758/s13428-010-0049-5

Nielsen, R., Akey, J. M., Jakobsson, M., Pritchard, J. K., Tishkoff, S., & Willerslev, E. (2017). Tracing the peopling of the world through genomics. *Nature*, *541*, 302–310. https://doi.org/10.1038/nature21347

Padilla-Iglesias, C., Xue, Z., Leonardi, M., Paijmans, J. L. A., Colucci, M., Hovhannisyan, A., Maisano-Delser, P., Blanco-Portillo, J., Ioannidis, A. G., Lucarini, G., Cerasoni1, J. N., Kandel, A. W., Will, M., Hallett, E. Y., Lupo, K., Scerri, E. M. L., Crevecoeur, I., Vinicius, L., Migliano, A. B., Manica, A. (2025). *Pan-African metapopulation model explains Homo sapiens genetic and morphological evolution*. bioRxiv. https://doi.org/10.1101/2025.05.22.655514

Pemberton, T. J., DeGiorgio, M., & Rosenberg, N. A. (2013). Population structure in a comprehensive genomic data set on human microsatellite variation. *G3: Genes, Genomes, Genetics*, *3*(5), 891–907. https://doi.org/10.1534/g3.113.005728

Pickrell, J. K., Patterson, N., Loh, P.-R., Lipson, M., Berger, B., Stoneking, M., Pakendorf, B., & Reich, D. (2014). Ancient west Eurasian ancestry in southern and eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(7), 2632-2637. https://doi.org/10.1073/pnas.1313787111

Pickrell, J. K., & Reich, D. (2014). Toward a new history and geography of human genes informed by ancient DNA. *Trends in Genetics*, *30*(9), 377-389. https://doi.org/10.1016/j.tig.2014.07.007

Prugnolle, F., Manica, A., & Balloux, F. (2005). Geography predicts neutral genetic diversity of human populations. *Current Biology*, *15*(5), R159–R160. https://doi.org/10.1016/j.cub.2005.02.038

Quilodrán, C. S., Rio, J., Tsoupas, A., & Currat, M. (2023). Past human expansions shaped the spatial pattern of Neanderthal ancestry. *Science Advances*, *9*(42), Article eadg9817. https://doi.org/10.1126/sciadv.adg9817

R Core Team (2021). *R: A Language and Environment for Statistical Computing (*Version 4.0.5) [Computer software]. https://www.R-project.org

Ragsdale, A. P., Weaver, T. D., Atkinson, E. G., Hoal, E. G., Möller, M., Henn, B. M., & Gravel, S. (2023). A weakly structured stem for human origins in Africa. *Nature*, *617*, 755–763. https://doi.org/10.1038/s41586-023-06055-y

Ramachandran, S., Deshpande, O., Roseman, C. C., Rosenberg, N. A., Feldman, M. W., & Cavalli-Sforza, L. L. (2005). Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(44), 15942–15947. https://doi.org/10.1073/pnas.0507611102

Relethford, J. H., & Blangero, J. (1990). Detection of differential gene flow from patterns of quantitative variation. *Human Biology*, *62*(1), 5–25.

Rito, T., Vieira, D., Silva, M., Conde-Sousa, E., Pereira, L., Mellars, P., Richards, M. B., & Soares, P. (2019). A dispersal of Homo sapiens from southern to eastern Africa immediately preceded the out-of-Africa migration. *Scientific Reports*, *9*, Article 4728. https://doi.org/10.1038/s41598-019-41176-3

Savin, N. E., & White, K. J. (1977). The Durbin-Watson test for serial correlation with extreme sample sizes or many regressors. *Econometrica*, *45*(8), 1989–1996. https://doi.org/10.2307/1914122

Scerri, E. M. L., Chikhi, L., & Thomas, M. G. (2019). Beyond multiregional and simple out-of-Africa models of human evolution. *Nature Ecology & Evolution*, *3*, 1370–1372. https://doi.org/10.1038/s41559-019-0992-1

Schlebusch, C. M., Sjödin, P., Breton, G., Günther, T., Naidoo, T., Hollfelder, N., Sjöstrand, A. E., Xu, J., Gattepaille, L. M., Vicente, M., Scofield, D. G., Malmström, H., de Jongh, M., Lombard, M., Soodyall, H., & Jakobsson, M. (2020). Khoe-San genomes reveal unique variation and confirm the deepest population divergence in *Homo sapiens*. *Molecular Biology and Evolution*, *37*(10), 2944–2954. https://doi.org/10.1093/molbev/msaa140

Schlebusch, C. M., Skoglund, P., Sjödin, P., Gattepaille, L. M., Hernandez, D., Jay, F., Li, S., De Jongh, M., Singleton, A., Blum, M. G. B., Soodyall, H., & Jakobsson, M. (2012). Genomic variation in seven Khoe-San groups reveals adaptation and complex African history. *Science*, *338*(6105), 374–379. https://doi.org/10.1126/science.1227721

Semo, A., Gayà-Vidal, M., Fortes-Lima, C., Alard, B., Oliveira, S., Almeida, J., Prista, A., Damasceno, A., Fehn, A.-M., Schlebusch, C., & Rocha, J. (2019). Along the Indian Ocean coast: Genomic variation in Mozambique provides new insights into the Bantu expansion. *Molecular Biology and Evolution*, *37*(2), 406–416. https://doi.org/10.1093/molbev/msz224

Skoglund, P., & Jakobsson, M. (2011). Archaic human ancestry in East Asia. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(45), 18301-18306. https://doi.org/10.1073/pnas.1108181108

Skoglund, P., Thompson, J. C., Prendergast, M. E., Mittnik, A., Sirak, K., Hajdinjak, M., Salie, T., Rohland, N., Mallick, S., Peltzer, A., Heinze, A., Olalde, I., Ferry, M., Harney, E., Michel, M., Stewardson, K., Cerezo-Román, J. I., Chiumia, C., Crowther, A., … Reich, D. (2017). Reconstructing prehistoric African population structure. *Cell*, *171*(1), 59–71. https://doi.org/10.1016/j.cell.2017.08.049

Sugden, L. A., & Ramachandran, S. (2016). Integrating the signatures of demic expansion and archaic introgression in studies of human population genomics. *Current Opinion in Genetics & Development*, *41*, 140–149. https://doi.org/10.1016/j.gde.2016.09.007

Tierney, J. E., deMenocal, P. B., & Zander, P. D. (2017). A climatic context for the out-of-Africa migration. *Geology*, *45*(11), 1023–1026. https://doi.org/10.1130/G39457.1

Tishkoff, S. A., Reed, F. A., Friedlaender, F. R., Ehret, C., Ranciaro, A., Froment, A., Hirbo, J. B., Awomoyi, A. A., Bodo, J.-M., Doumbo, O., Ibrahim, M., Juma, A. T., Kotze, M. J., Lema, G., Moore, J. H., Mortensen, H., Nyambo, T. B., Omar, S. A., Powell, K., … Williams, S. M. (2009). The genetic structure and history of Africans and African Americans. *Science*, *324*(5930), 1035–1044. https://doi.org/10.1126/science.1172257

Van Tuyl, R., & Pereltsvaig, A. (2012). Comment on "Phonemic Diversity Supports a Serial Founder Effect Model of Language Expansion from Africa". *Science*, *335*(6069), Article 657-d. https://doi.org/10.1126/science.1209176

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

von Cramon-Taubadel, N., & Lycett, S. J. (2008). Brief communication: Human cranial variation fits iterative founder effect model with African origin. *American Journal of Physical Anthropology*, *136*(1), 108–113. https://doi.org/10.1002/ajpa.20775

Williams, E. (2011). *Aviation formulary V1.46*. http://edwilliams.org/avform.htm