Modern humans dispersed from southern 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 and spread to the other habitable continents. It is unclear if we expanded across Africa, however, this manuscript highlights methodological issues in previous research on the topic. Moreover, we are known to lack clarity on where the expansion would have begun. 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). For each diversity, i) it was examined if there is a geographical pattern within Africa and ii) the best choices for the origin of the expansion were estimated. A ranking procedure indicated, across diversities, where the expansion originated. Each diversity declined with increasing distance from somewhere inside of 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 indicated an expansion from southern Africa. Admixture is a known obstacle for using diversity to study expansion. It is explained why results might not have arisen from a broad effect of admixture given that i) linkage disequilibrium previously pointed to the south and ii) supplementary analysis with additional measures (which should not broadly be affected by admixture) tentatively indicated a southern origin.

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). Across-Africa expansion 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); finding the origin of across-Africa expansion may be crucial for precisely locating where out-of-Africa expansion began (e.g., Henn et al., 2012). 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 including its origin.

Population bottlenecks

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, effective population size falls and genetic drift increases (e.g., Fortes-Lima et al., 2024; Li et al., 2008; 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). Consistent with out-of-Africa expansion, this trend in diversity/LD occurs as distance from Africa increases (when diversity/LD is from populations across the globe) (e.g., Jakobsson et al., 2008; Ramachandran et al., 2005). The trend in genetic diversity is echoed in cranial diversity (Betti et al., 2009; von Cramon-Taubadel & Lycett, 2008).

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 which an analysis uses, and ii) the location/point from which we measure geographical distance (Table 1; Cenac, 2022b). 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 attempted (*Method*).

A previous study, Schlebusch et al. (2012), examined geographical variation in biological variables (which are stated in the second row of 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 of Schlebusch et al. (2012) would be insensitive to detecting patterns and an origin. The Fortes-Lime et al. 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) may be compounded by them having used fewer than half as many populations as Fortes-Lima et al. (2024) (also see Table 1).

Admixture

Even if expansion spread to areas which were already populated, and admixing happened (Henn et al., 2018), a bottleneck-consistent signal can still be detected in diversity and LD, as we can see when it comes to the Bantu expansion (Fortes-Lima et al., 2024), which notably changed the genetic landscape of Africa (e.g., Fortes-Lima et al., 2024; Skoglund et al., 2017). Nonetheless, admixture is an issue for identifying the origin of the across-Africa expansion (e.g., Colonna et al., 2011). Admixture can obscure an expansion signal (Hunley & Cabana, 2016) or a bottleneck-congruent expansion pattern (e.g., the decrease of diversity) may, to some extent, be caused by events which happened after expansion—later migration and admixture (e.g., Skoglund & Mathieson, 2018); admixture could affect estimation of where across-Africa expansion originated (e.g., Colonna et al., 2011). Admixture increases diversity (Bergström et al., 2021) usually, although not necessarily (Haber et al., 2016), and admixture also increases LD (Henn et al., 2011). As distance from the supposed origin increases, 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, whereas they affect LD in the *same* direction. Therefore, if diversity and LD were to indicate the same region as the origin (Colonna et al., 2011), then it would be unlikely that a general effect of admixture is the reason for that region being indicated. LD has indicated a southern origin (Henn et al., 2011; but see Table 1); if diversity within sub-Saharan Africa broadly suggests a southern origin, then a general effect of admixture may seem unlikely to be the cause. Moreover, we can look beyond diversity and LD to infer the origin of across-Africa expansion (Henn et al., 2011), as the current study did to an extent (Table 2; *Method*).

This study

The present study examined the across-Africa expansion, principally 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 each diversity, and searched for the origin indicated by *each*

diversity and *across* diversities (*Method*). The number of populations used for each diversity (*Method*), compared to when populations are used from across the globe (Balloux et al., 2009; Betti et al., 2009), was quite few (also see Table S4); this was mitigated by analysis which concurrently considered the diversities when estimating the origin.

Table 1

Across-Africa Expansion: Trends?

Study	Variable	Findings and thoughts
Henn et al. (2011)	Linkage disequilibrium	• In Henn et al. (2011), using 25 population datapoints, the across-Africa expansion seemed to have begun in southern-southwestern Africa, e.g., linkage disequilibrium increased with distance from southwestern Africa. • In other research, a variable found from linkage disequilibrium (Schlebusch et al., 2012) did not indicate an origin (López et al., 2015) (but see the next row in the present table).
Schlebusch et al. (2012)	Various	• In Schlebusch et al. (2012), haplotype diversities (richness and heterozygosity) had no patent geographical pattern, and a regional origin of across-Africa expansion was not suggested via the diversities, runs of homozygosity, and a variable derived from linkage disequilibrium. • Supplementary material in Schlebusch et al. (2012) indicates that they only used about 20 populations for each variable. Compared to analyses with populations globally (Prugnolle et al., 2005; Ramachandran et al., 2005), 20 is low. Yet, through calculations in G*Power (Faul et al., 2009), we can see that even 20 populations *can* be sufficient for detecting a significant *out-of-Africa* trend in genetic diversity if we use populations across the globe (Table S4). Nevertheless, limiting analysis to one continent results in a loss of statistical power when it comes to a bottleneck-consistent signal (Atkinson, 2012). • 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 in Hunley and Cabana (2016). • However, in a preprint, a significant decrease in autosomal heterozygosity (of sub-Saharan Africans) 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, 2022b). Detection of a pattern in linkage disequilibrium within Africa is also affected by which *origin* is used (Henn et al., 2011).

Note. Each of the three studies (column 1) used Holocene data (Henn et al., 2011; Hunley & Cabana, 2016; Schlebusch et al., 2012; Tishkoff et al., 2009; Pemberton et al., 2013).

Estimating the origin (through diversity) may be affected by admixture (Colonna et al., 2011). Consequently, it would be useful to explore the origin of across-African expansion when the effect of admixture is minimised (e.g., Henn et al., 2011). Therefore, as a step towards addressing a possible effect of admixture (e.g., Colonna et al., 2011), a further two variables (phylogenetic tree branch lengths and cranial sexual size dimorphism) (Table 2), were tentatively used in post-hoc analysis to supplement findings with diversity regarding the origin of across-Africa expansion.

Table 2

Alternative Variables to Address Admixture

Variable	Findings and thoughts
Branch length in a phylogenetic tree	• The pattern of a phylogenetic tree is congruent with out-of-Africa expansion (Li et al., 2008) and the length of phylogenetic tree branches (from root to population) greatens as heterozygosity declines (Pickrell & Pritchard, 2012) and are associated with effective population size (Li et al., 2008). Whilst Li et al. (2008) state that the correlation between branch length and effective population size has a Spearman's rho of .82, a reanalysis of data from Li et al. (2008) shows that the correlation coefficient is actually negative (-.82). • Therefore, we would expect branch length to i) increase with distance from Africa and, ii) indicate the origin of across-Africa expansion. • Whilst admixture between populations would decrease the lengths of branches between these populations in a phylogenetic tree (Li et al., 2008; Tishkoff et al., 2009), there is no patent reason for why a greater level of admixture should broadly decrease or increase the branch length of a population (with length being between root and population).
Cranial sexual size dimorphism	• The sexual size dimorphism of the cranium i) appears to mark out-of-Africa expansion, ii) should not generally greaten/lessen with admixture, and iii) when concurrently using a number of variables to find the origin of out-of-Africa expansion, cranial sexual size dimorphism confers support to the south (Cenac, 2022b, 2024).

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

Cranium

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) to the knowledge of the author; in the present study, male crania and female crania were not studied simultaneously when it came to diversity. In the context of studies on across-Africa expansion (e.g., Henn et al., 2011; Schlebusch et al., 2012), even 13 populations are few (also see Table S4). However, because more sub-Saharan African populations were available for males than for females (Howells, 1989, 1996; Manica et al., 2007), only male crania were used when calculating cranial diversity. 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. Like before (von Cramon-Taubadel & Lycett, 2008), within-population cranial shape diversity was calculated in RMET 5.0 (Relethford & Blangero, 1990). Principal coordinates analysis was used in RMET (Relethford & Blangero, 1990) on the cranial shape dimensions.

Cranial sexual size dimorphism has been calculated by i) finding the average cranial size (from geometric means) for different populations, amongst males and amongst females, ii) dividing the average male cranial size by the average female cranial size, and iii) calculating the natural log of that division (Cenac, 2022a, 2022b); in the present study, that method was used to calculate cranial sexual size dimorphism for each of eight Holocene sub-Saharan African populations using male and female crania from Howells (1989, 1996) and Manica et al. (2007) datasets (Table S1). This was done using the 11 dimensions which appear to be defined the same in Howells and Hanihara data (Algee-Hewitt, 2011; Figure 1).

Genetic

Balloux et al. (2009) analysed mitochondrial DNA. This DNA represented the contemporary situation for the mitochondrial DNA of modern humans across the planet (Balloux et al., 2009). 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, 2022b); 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 (Mallick et al., 2016). Mallick et al. (2016) calculated these diversities 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 diversity 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 of those two diversities was controlled for minimum temperature (but, see *Discussion*).

Out-of-Africa expansion has previously been studied through i) cranial diversity by way of the data in Manica et al. (2007) (e.g., Betti et al., 2009) or the Howells data (e.g., von Cramon-Taubadel & Lycett), and ii) mitochondrial diversity derived from HVRBase++ data (Balloux et al., 2009). Geographical trends in heterozygosity have been explored through Simons Genome Diversity Project data (Watkins et al., 2020). However, to the knowledge of the author, no previous study had used these cranial and genetic data to examine if there is geographical variation in the diversity of sub-Saharan Africans specifically which is congruent with across-Africa expansion.

Phylogenetic tree branch lengths of six sub-Saharan populations from the HGDP-CEPH data (Li et al., 2008) were used in the current study. HGDP-CEPH data represent current populations (e.g., Bergström et al., 2020). There are different ways in which phylogenetic trees can be constructed, e.g., through neighbour joining and maximum likelihood methods (Kuhner & Felsenstein, 1994). Li et al. (2008) present branch lengths (in units) calculated from neighbour joining and maximum likelihood methods, and they constructed trees using those methods. In the present study, branch lengths from the maximum likelihood method were initially the only branch lengths which were used (in

supplementary analysis). This was because Li et al. (2008) utilised that method in the only phylogenetic tree which they present in their journal article. Moreover, branches from the maximum likelihood method were prioritised because, of the two methods, maximum likelihood generally seems to be the better one (Kuhner & Felsenstein, 1994), and because of additional reasoning given in the note of Figure S4.

To minimise the influence of non-African gene flow, analysis can be restricted to sub-Saharan African populations (Cenac, 2022b), and that practice was applied in the current study for cranial and genetic diversities, tree branch lengths, and cranial sexual size dimorphism.

Sufficiency of the number of populations

Post-hoc, G*Power (Faul et al., 2009) indicated that the numbers of populations (in of themselves) should be sufficient to find a true geographical pattern in the types of genetic diversity, but not quite sufficient (although close) in the case of cranial shape diversity (Table S4). If G*Power had been used before correlation tests were run, then cranial shape diversity would not have been used in this study to explore across-Africa expansion. Moreover, testing in G*Power was based on using populations globally (Table S4); restricting analysis to a continent decreases power (Atkinson, 2012), and so, the estimates of the required number of populations (Table S4) is likely to be too low. Through G*Power, the necessary number of populations for a correlation test would be 15 and seven respectively for cranial sexual size dimorphism and tree branch lengths (Table S4), i.e., more than the totals used in the present study.

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, 2022b) 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, 2022b; 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, iii) for an impression of where cranial shape dimensions suggest the origin is, and iv) for an overall indication of the origin from branch lengths in phylogenetic trees and cranial sexual size dimorphism. The design of Figures 1D, 2A, 2C, 2D, 3, S1, S2, S4, and S5B have a basis in the designs of figures in preprints, and those designs in the preprints have some basis on a figure from Betti et al. (2013) (Cenac, 2022b; 2023a).

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) in the current study. 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 in R. 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).

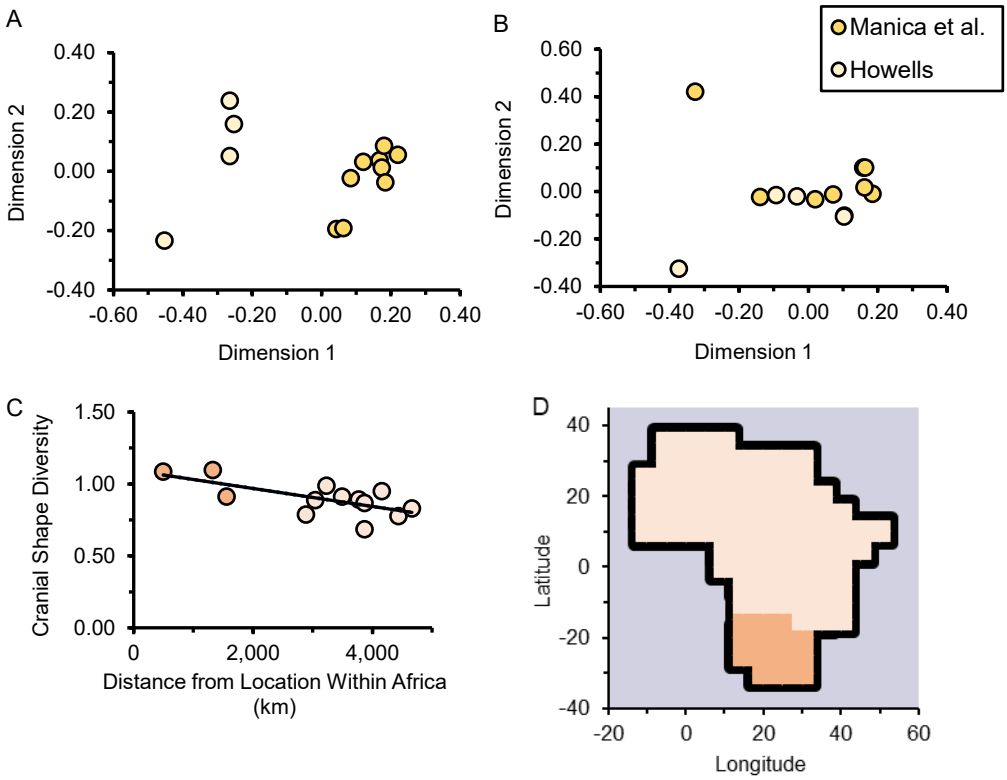
Results

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, in the present study, 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.

Figure 1

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



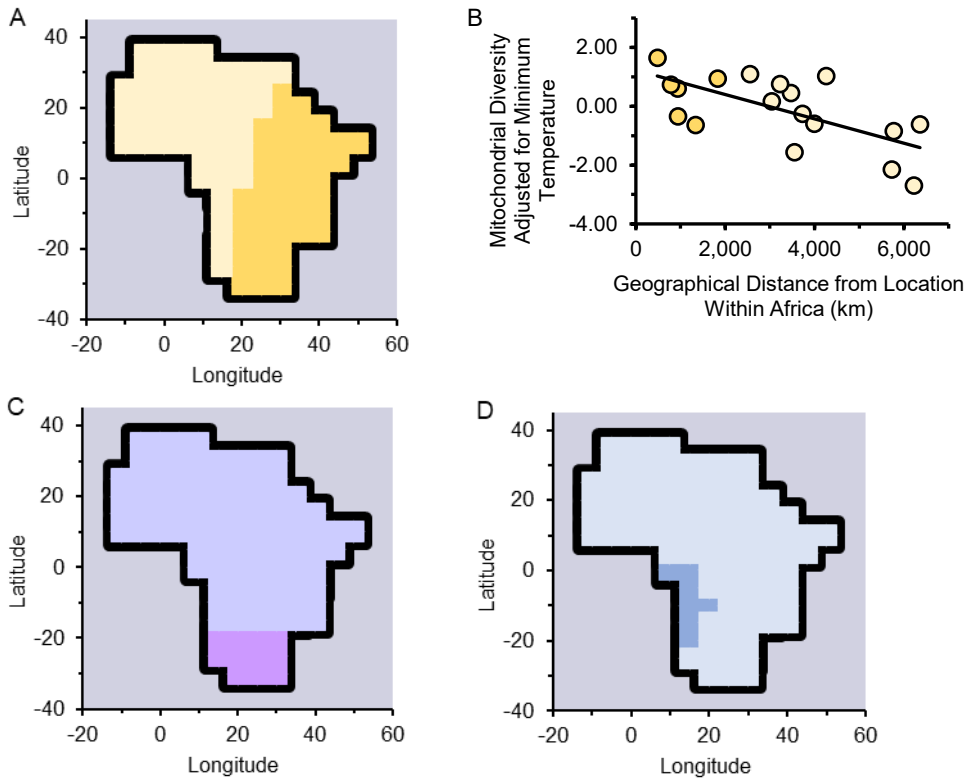
Note. Figure 1A and 1B represent dimensions from principal coordinates analysis. In Figure 1A, Dimensions 1 and 2 respectively captured 50.3% and 19.0% of the interpopulation variation in cranial shape. Dimension 1 separated the Howells data (less than -.20) from the Manica et al. (2007) data (above 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.

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, 2022b; Manica et al., 2007); a ranking procedure (see *Method*) did not indicate that a small proportion of the dimensions drove results (Figure S1; Table S2). Some cranial dimensions do not decline in (form) diversity with the rise in distance from Africa (Manica et al., 2007). Out of the 11 cranial dimensions which are common to the Howells and Manica et al. data (Table S2), eight exhibit a decline (Manica et al., 2007; see Table S2). In case only those eight dimensions (of the 11) truly reflect out-of-Africa expansion,

some of the analyses with the 11 dimensions was repeated using just those eight. Clearly, eight dimensions is a considerable drop from the intended 25 dimensions. However, the out-of-Africa expansion has been explored (for a section of the skeleton) with fewer than eight dimensions before (Betti & Manica, 2018; Betti et al., 2012). For instance, three dimensions have been used when it comes to pelvic shape diversity (Betti et al., 2012). When using the eight cranial dimensions alone, the correlation between the shape diversity of the cranium and distance from southern Africa (25°S, 15°E) became numerically larger (r = -.78; Figure 5A) than when 11 dimensions were used, and the origin of expansion was still suggested to be southern Africa (Figure S5B).

Figure 2

Genetic Diversity and the Origin of Across-Africa Expansion



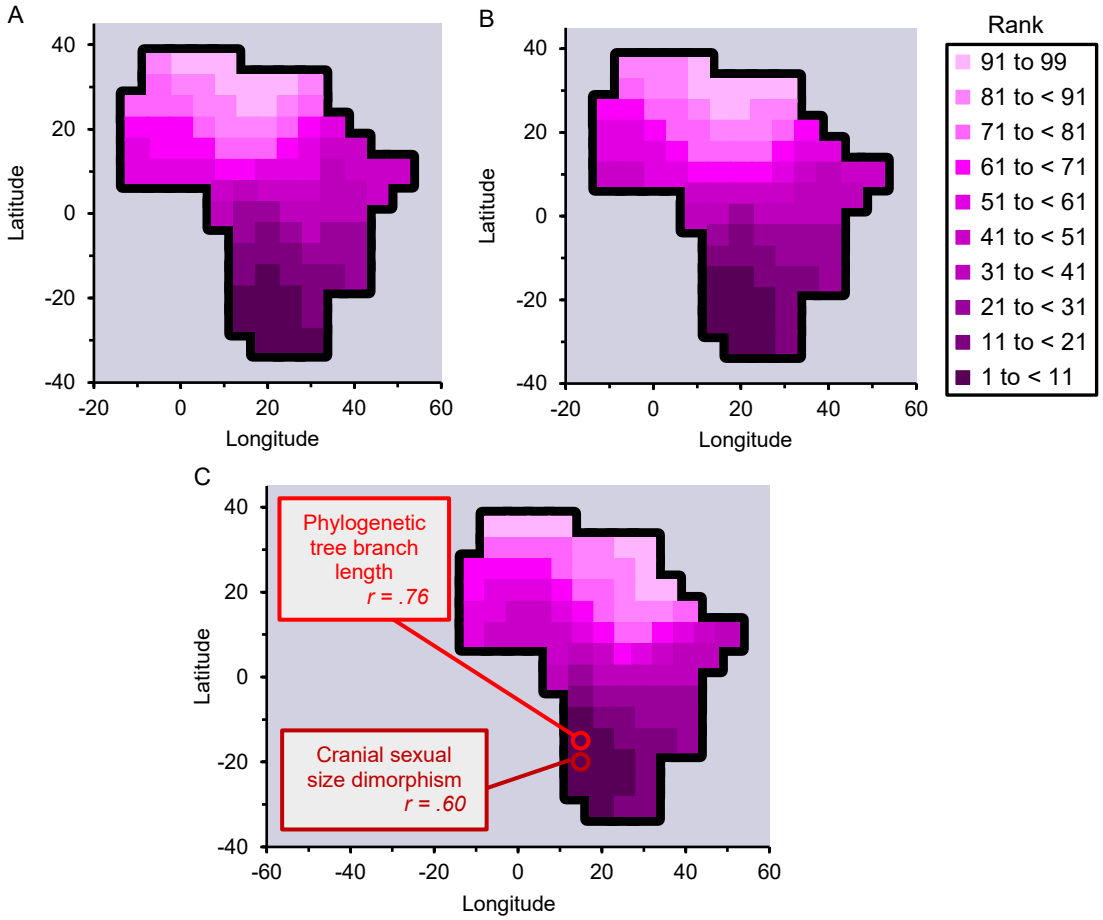
Note. Figure 2A and 2B are regarding (adjusted) mitochondrial diversity, whilst Figure 2C and 2D are for X-chromosomal diversity and autosomal diversity respectively. In each map, the darker-shaded area indicates a geographical area amongst which the across-Africa expansion originated (Figure 2A, 2C, and 2D). Mitochondrial diversity pointed to a noticeably larger geographical range of possible origins than cranial, X-chromosomal, and autosomal 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 because southern African populations were not used.

Genetic diversities

Genetic diversities (Balloux et al., 2009; Mallick et al., 2016) exhibited patterns 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.

Figure 3

Estimating the Origin of Across-Africa Expansion Across Measures



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. Figure 3C used the lengths of branches in phylogenetic trees alongside cranial sexual size dimorphism. Figure 3C highlights the location that yield the highest correlation coefficient for the potential association between distance and i) branch length (maximum likelihood method) and ii) cranial sexual size dimorphism.

Indicating the origin when simultaneously considering variables

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). A southern origin was further supported by phylogenetic tree branch lengths and cranial sexual size dimorphism jointly pointing to a southern African origin (Figure 3C). However, when branch lengths from the neighbour joining method were used (Figure S4), results in the present study were markedly different than when branch lengths were from the maximum likelihood procedure (Figure 3C); the origin potentially indicated seems to vary to a notable level based on the method. Nevertheless, as stated in the *Method*, results found through the maximum likelihood method were favoured given that previous research suggested that the maximum likelihood method is the better method (over neighbour joining) (Kuhner & Felsenstein, 1994), and the deliberation covered in the note of Figure S4.

Autosomal diversity: Follow-up

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).

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. Therefore, it is now clear that diversity within Africa is compatible with an across-Africa expansion. Southern and eastern Africa are the most promising options for the origin (Henn et al., 2018), and the current study points to southern Africa (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 a stage of the broader out-of-Africa expansion (Hallett et al., 2025; Henn et al., 2018), then the origin of across-Africa expansion *is* the origin of out-of-Africa expansion (Henn et al., 2012; Tishkoff et al., 2009); the present study suggests that out-of-Africa expansion originated in the south.

Admixture

Admixture affects diversity and LD (Bergström et al., 2021; Haber et al., 2016; Henn et al., 2011), which means that admixture can affect estimation of the origin (Colonna et al., 2011). However, as explained in the *Introduction*, 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) does indeed suggest that admixture is not the reason for why diversities, in the present study, marked out a southern origin (Figure 3). On the other hand, in a previous study, 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, that study was Schlebusch et al. (2012), and, as noted above, their method for indicating origins may not have been sensitive. The southern estimate (Figure 3) was bolstered by the origin indicated by phylogenetic tree branch lengths and cranial sexual size dimorphism (Figure 4)—admixture should not generally affect where those variables suggest the origin is (Table 2). This congruency between diversities and non-diversities bodes well for admixture not being the reason why a southern origin is indicated by diversities.

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). Clearly, 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 3).

Limitations

Drawing on the literature (e.g., Amos, 2020; Balloux, 2009), limitations to this study are considered, centring on i) admixture and ii) X-chromosomal diversity and climate.

Admixture: Addressing a broad effect?

It would be useful to explore the origin of across-Africa expansion by continuing to use variables other than diversity in order to address admixture (e.g., Henn et al., 2011). In Fortes-Lima et al. (2024), LD was calculated for far more sub-Saharan African populations than either Henn et al. (2011) or Schlebusch et al. (2012). Moreover, it should be noted that whilst Fortes-Lima et al. (2024) examined if there is a geographical pattern in LD for Bantu-speaking populations, they also calculated

LD for sub-Saharan African populations outside of Bantu-speaking ones; it could be helpful to see where LD suggests the across-Africa expansion originated by using the data employed in Fortes-Lima et al. As for branch lengths, it is possible to include gene flow episodes in a phylogenetic tree, which improves how well the tree captures genetic variation (Pickrell & Pritchard, 2012); branch lengths, with the inclusion of gene flow, could be used to identify the origin of the expansion.

Table 3

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).

In the present study, there were too few populations for useful correlation tests to be run using phylogenetic tree branch lengths or cranial sexual size dimorphism (Table S4). So, whilst correlation coefficients for those two variables (Figure 3C) are consistent with there being expansion from southern Africa, conclusions must remain tentative for now regarding whether a broad effect of admixture underlies why diversities indicated a southern origin. Therefore, it would be useful if future research used those variables to explore across-Africa expansion. When it comes to available genetic data (Pemberton et al., 2013), phylogenetic tree branch lengths can be calculated (Li et al., 2008) for far more sub-Saharan African populations than the number used in the present study (see Pemberton et al., 2013). Unfortunately, for the cranium, the number of populations for which measurements of sub-Saharan Africans are available for males and females (Howells, 1989, 1996; Manica et al., 2007) is limited (Table S4).

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 to lessen an impact of admixture from the not-so-distant past). A similar approach could be used regarding across-Africa expansion in order to reduce any effect of admixture.

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 in future research (e.g., Ragsdale et al., 2023), which the present study did not do.

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. In the data used in the current study (regarding autosomal diversity), Somalis were only represented by one individual, and 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 results were due to a combination of the across-Africa signal and 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, the autosomal microsatellite heterozygosity of sub-Saharan African populations indicated a southern origin (in analysis where 106 populations were utilised) (Cenac, 2022b).

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 to 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, as may phylogenetic tree branch lengths and cranial sexual size dimorphism (Figure 3). Therefore, findings in this study could, to some level, help address a broad effect of admixture on the estimation of the origin (*Admixture*). However, the effect of admixture could be addressed more thoroughly (*Admixture: Addressing a broad effect?*). Moreover, it

is questionable if Khoe-San were involved early in this expansion (Table 3), 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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